Chapter 5
ROOT STRATEGIES FOR PHOSPHORUS ACQUISITION

Jonathan P. Lynch and Kathleen M. Brown

LOW SOIL P AVAILABILITY IS A PRIMARY CONSTRAINT TO PLANT PRODUCTIVITY

Soil infertility is a primary constraint to plant productivity over the majority of the earth's land surface. Nitrogen is often limiting in young soils of the temperate zone, while phosphorus (P) is a primary limitation in most forests, weathered soils and the humid tropics, which support the majority of terrestrial plant biomass (Walker 1965; Lynch and Deikman 1998; Figure 5.1). Low soil P availability is caused by several factors, including the reactivity of orthophosphate (Pi) with common soil constituents such as Fe and Al oxides, resulting in compounds of limited bioavailability, especially as soil weathering progresses, and the open-ended P cycle that tends towards depletion. Human activity in many managed ecosystems has reduced P bioavailability further through topsoil erosion, acidification, and nutrient mining, especially in developing countries (Hartemink 2003). Approximately 50% of the agricultural soils in the world have been degraded significantly by human activity, including 75% of the agricultural soils of Africa (Oldeman *et al*. 1991; Wood *et al*. 2000). Replenishment of soil P reserves through fertilization is common in developed countries, but the economic sustainability of this practice is in question, as economically recoverable P reserves are estimated to be 50% depleted by the middle of this century (Steen 1998; Abelson 1999). In many developing countries, especially in Africa, fertilizer use is negligible (World Bank 2004), and the productivity of many of these agroecosystems is P-limited. The development of crops and cropping systems with greater productivity on soils of low P bioavailability would substantially improve global food security (Lynch 2007). The response of terrestrial ecosystems to global climate change will depend on interactions of climate change variables with edaphic limitations to plant productivity, including P (Lynch and St. Clair 2004). The adaptation of plants to low P availability is therefore of considerable interest in both basic and applied plant biology.

P.J. White, J.P. Hammond (eds.) *The Ecophysiology of Plant-Phosphorus Interactions*,

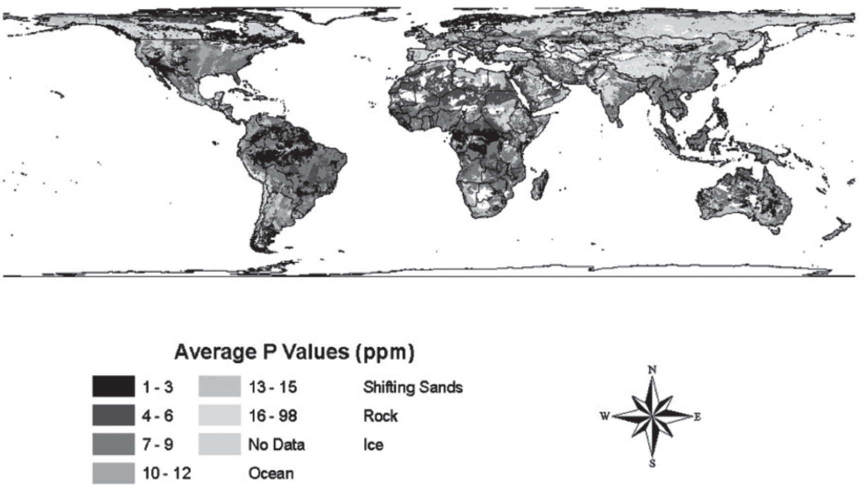

Fig. 5.1 Map of soil phosphorus availability. (Jaramillo and Lynch, unpublished, 2008.)

PHOSPHORUS IS AN IMMOBILE SOIL NUTRIENT

The large majority of P taken up by plant roots is in the form of orthophosphate (Pi; Smith *et al*. 2003). Because of its reactivity with many chemical and biological components of the soil, only a small part of the total P content of the soil occurs as Pi (Comerford 1998), and movement of Pi in the soil solution is slow. Transport of Pi through mass flow of water to the root surface is negligible, and diffusion of Pi in soils is typically in the order of fractions of a millimeter per day (Barber 1962, 1995). Phosphorus uptake creates ‘depletion zones’ around the root with little bioavailable P, that will only slowly recharge through diffusion and mineralization (Hinsinger *et al*. 2005). This makes P the most immobile, and often the least bioavailable, of the macronutrients. The immobility of P in soil typically results in large spatial variation in P bioavailability. Mature soils display large vertical gradients in P content and bioavailability, caused by continual deposition of P on the soil surface in shoot residues, and greater organic matter content, biological activity, and P turnover in the topsoil (Lynch and Brown 2001). Spatial variation in P bioavailability may also be created by soil fauna, especially ants and termites. A fundamental challenge in plant acquisition of P is the need to explore a heterogeneous substrate and the need to place roots or root symbionts within millimeters of fresh P sources that have not already been depleted.

ROOT TRAITS ARE KEY ADAPTATIONS TO LOW P AVAILABILITY

We focus here on root strategies for P-acquisition. By 'strategy' we mean traits or sets of traits that have adaptive value in acquiring P. By 'trait' we mean a 'phene' as a distinct element of an organism's phenotype. Just as a genotype is comprised of many distinct genes, a phenotype is comprised of many distinct phenes. Phenes are generally more abstract and indistinct than genes, and have received less research attention, but phenes rather than genes determine fitness. Phenes rather than genes are subject to selection in plant domestication, and even today, are the basis of the vast majority of crop breeding. As an example of a phene that is important for P-acquisition, root hair length is a phene controlled by multiple genes. Intraspecific variation for root hair length is an important determinant of P-acquisition (see below). The adaptive value of phenes may be affected by interactions with other phenes. In the case of root hairs, root hair length has strong synergism with root hair density (i.e. number of root hairs per unit root epidermal surface area) for P acquisition (Ma *et al*. 2001b). This type of synergism is useful to consider in the context of an 'integrated phenotype', i.e. a set of phenes whose interactions determine fitness in a particular environment. We consider a phene or integrated phenotype that enhances P-acquisition a 'strategy'. The identification of adaptive strategies, and an understanding of the physiological and ecological tradeoffs associated with them, are essential in understanding plant adaptation to P-limited ecosystems. This is especially important for breeding more P-efficient crops, an enterprise of great importance for global food security (Lynch 2007).

Given the low bioavailability and mobility of P in most soils, the ability of root systems to explore effectively the soil and exploit the rhizosphere, at minimal metabolic cost, is essential to plant fitness. Roots display a variety of adaptations to low P availability (Lynch and Brown 2006), including mycorrhizal symbioses (Smith and Read 1997), root hair elongation and proliferation (Bates and Lynch 1996; Ma *et al*. 2001a,b), rhizosphere modification through secretion of organic acids (Jones 1998; Ryan *et al*. 2001), protons (Hinsinger 2001), and phosphatases (Hayes *et al*. 1999), and modification of root architecture to maximize P acquisition efficiency (Figure 5.2; Lynch and Brown 2001; Lynch 2005; George and Richardson 2008; Kirkby and Johnston 2008; Vance 2008; White and Hammond 2008). Phosphorus-deficient plants typically have higher root to shoot ratios than high-P plants, either because of allometric relationships (Niklas 1994) or because of increased biomass allocation to roots (Gutschick 1993; Nielsen *et al*. 2001). Increased root growth is obviously beneficial for P-acquisition, but can slow overall plant growth because of the increased respiratory burden of root tissue (Van der Werf *et al*. 1992; Hansen *et al*. 1998; Nielsen *et al*. 1998, 2001; Lynch and St. Clair 2004).

These topics encompass several active fields of research with large literatures that cannot be adequately reviewed here. Several recent reviews summarize plant responses to low P availability, emphasizing cellular and biochemical or molecular

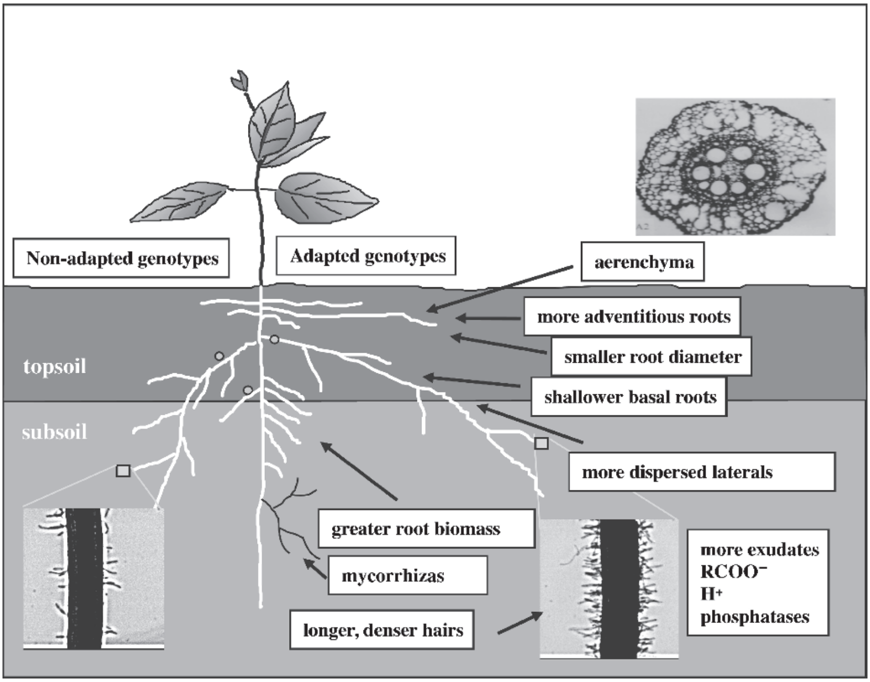

Fig. 5.2 Changes in root architecture, morphology, and anatomy associated with adaptation to low phosphorus in common bean

processes (Abel *et al*. 2002; Vance *et al*. 2003; Ticconi and Abel 2004; Tesfaye *et al*. 2007), and specific adaptations to low P availability, such as cluster roots (Diem *et al*. 2000; Lamont 2003; Neumann and Martinoia 2002; Shane and Lambers 2005; Lambers *et al*. 2006), mycorrhizas (Harrison 1999; Smith *et al*. 2003; Oldroyd *et al*. 2005) and rhizosphere modification (Hinsinger *et al*. 2003; Kochian *et al*. 2005). Our focus here is on strategies of the roots themselves, at the scale of the organ and organism, with particular attention to the functional importance of phenes involved with root growth and architecture for P-acquisition. While this subject has received less research attention than mycorrhizas, rhizosphere modification, cluster roots, and genetic responses to P stress, root growth and architecture have overarching importance at the organismal scale by determining the extent and localization of soil exploration, and by locating the expression of other root traits in specific soil domains.

BIOMASS ALLOCATION TO ROOTS

A common response of plants to P-deficiency is to increase their root to shoot dry-weight (DW) ratio, resulting from a greater inhibition of shoot growth than root growth (Whiteaker *et al*. 1976; Lynch *et al*. 1991; Mollier and Pellerin 1999).

A portion of this apparent change in root to shoot DW ratio is allometric, i.e. root: shoot ratios normally decline with growth, and since plants supplied with low P grow more slowly, their root to shoot ratios are higher at a given plant age. However, when this factor is eliminated by comparison of allometric coefficients among plants grown at different P levels, some genotypes show a greater allometric coefficient (larger increase in root DW relative to increases in shoot DW) with low P, while others do not. In the study of Nielsen *et al.* (2001), genotypes of common bean that were P-efficient (less yield depression under low P) maintained a higher root to shoot ratio (higher allometric coefficient) with continued growth, supporting the idea that root growth is valuable for P acquisition. Low P availability reduces leaf appearance, leaf expansion, and shoot branching (Radin and Eidenbock 1984; Lynch *et al.* 1991). Among annual plants, P-stress decreases shoot growth in dicots more than in monocots, possibly because of differences in leaf morphology (Halsted and Lynch 1996).

Root growth is a key trait for optimizing the efficiency of P acquisition and use in plants (Lynch 1995; Manske *et al.* 2000). Low P availability changes the distribution of growth among various root types. In common bean, growth of main root (primary and basal root) axes was maintained under low P, while initiation of lateral roots is reduced, so that lateral root density declines (Borch *et al.* 1999). Mean lateral root length was unaffected. In experiments with maize subjected to P-starvation, axile (seminal and nodal) root elongation and lateral root density were unaffected, but lateral root elongation was first promoted slightly, then severely retarded, as P-starvation proceeded (Mollier and Pellerin 1999). Initiation of new axile roots also ceased after six days of P-starvation. The maintenance of main root elongation in maize and bean could be interpreted as exploratory behavior, allowing these roots to grow maximally until they encounter localized patches of higher P availability. When the main root of a P-deficient plant encounters a patch of higher P availability, lateral roots may proliferate within the patch (see below; Robinson 2005). In Arabidopsis seedlings deprived of added P, lateral root number was also reduced, but in this case the remaining lateral roots elongated at the expense of the primary root (Williamson *et al.* 2001; Lopez-Bucio *et al.* 2002; Al-Ghazi *et al.* 2003). One reason for the discrepancy may be that Arabidopsis plants lack main roots other than the primary root (i.e. they have no root type analogous to the basal roots of legumes or the seminal roots of grasses), so that a subset of lateral roots must take over the functions of the other main roots in species with more complex root systems. We have observed genetic variation for the effect of buffered low P on lateral root length and number in maize, with some genotypes showing an increase and others showing a decrease in these variables (Zhu and Lynch 2004; Zhu *et al.* 2005a). Genotypes with increased or sustained lateral root development under P-deficiency had superior ability to acquire P and maintain growth.

In common bean, some genotypes preferentially increase growth of adventitious roots, which have the advantages of low construction cost and location in topsoil (see below; Miller *et al.* 2003; Ochoa *et al.* 2006). Adventitious rooting has long been associated with adaptation to waterlogging (Vartapetian and Jackson 1997) and has recently been associated with root rot resistance (Snapp *et al.* 2003; Roman-Aviles *et al.* 2004) and responses to root herbivory (Riedell and Reese

1999). In some crops, such as maize, a high proportion of the mature root system consists of adventitious roots, so prevention of adventitious rooting reduces water uptake even in well-watered plants (Jeschke *et al*. 1997). Under low P conditions, adventitious root development may be delayed or reduced, primarily as a result of overall growth inhibition (Pellerin *et al*. 2000; Miller *et al*. 2003; Ochoa *et al*. 2006). In some genotypes of bean, the maintenance of adventitious root formation, when overall growth is inhibited by P-deficiency, results in an increased proportion of root length in the adventitious root system (Miller *et al*. 2003). This characteristic was associated with plant P-efficiency traits in soils with poor P availability.

ROOT TRAITS AFFECTING SOIL EXPLORATION

Phosphorus distribution is highly heterogeneous in most soils, generally being greatest in surface horizons and decreasing with depth (Chu and Chang 1966; Anderson 1980; Pothuluri *et al*. 1986). The availability of soil P is also highly heterogeneous because of spatial heterogeneity of pH, eH, microbial activity, temperature, etc. (Barber 1995). Phosphorus mobilization and uptake by the root creates zones of P depletion that vary sharply on the scale of millimeters (Joner *et al*. 1995; Hinsinger *et al*. 2005). As a result of the development of P depletion zones around existing roots, P acquisition is highly dependent on continued root growth and exploration of new soil domains that have not yet been depleted of P (Barber 1995).

Topsoil exploration

Since the topsoil is generally the soil stratum with greatest P bioavailability, adaptation to low soil P availability is associated with the extent of topsoil foraging among genotypes of maize and bean (Bonser *et al*. 1996; Ge *et al*. 2000; Liao *et al*. 2001; Ho *et al*. 2005; Zhu *et al*. 2005b). We recently reviewed the importance of topsoil exploration for plant P-efficiency traits (Lynch and Brown 2001).

Architectural traits associated with enhanced topsoil foraging in common bean include shallower growth of basal roots, enhanced adventitious rooting, and greater dispersion of lateral roots (Figure 5.2). There are several lines of evidence that shallower basal root growth enhances topsoil foraging and thereby P acquisition efficiency. The geometric simulation model *SimRoot* was used to model the effect of changing basal root gravitropism on inter-root competition for P (Ge *et al*. 2000). This study showed that in soils with uniform P distribution, shallower root systems explored more soil per unit of root biomass than deeper systems, because shallower systems have more dispersed basal roots and therefore less inter-root competition, which occurs when neighboring roots have overlapping P depletion zones (Ge *et al*. 2000). In stratified soils with more P in the topsoil, the simulations showed that shallower root systems acquired more P than deep ones, by concentrating root

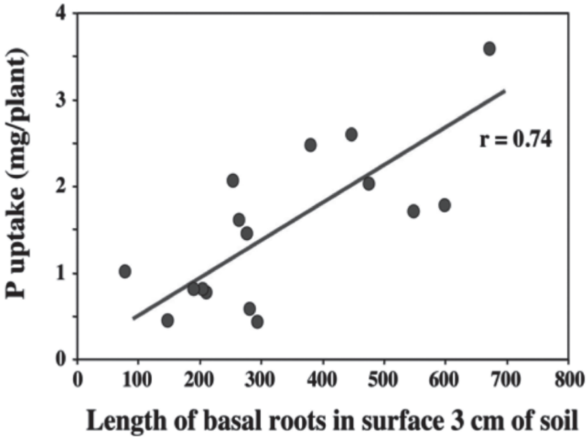

Fig. 5.3 Relationship between root shallowness and phosphorus uptake in recombinant inbred lines of common bean (*Phaseolus vulgaris* L.) growing in low-P soil. (Data extracted from Liao *et al.* (2001). With permission.)

foraging in the topsoil (Ge *et al.* 2000). These modeling results are supported by the significant correlation of basal root growth angle of young bean genotypes grown in growth pouches, with their yield in field trials in low P tropical soils (Bonser *et al.* 1996). In comparisons of individual plants grown in pots of soil, genotypes with shallower basal roots had greater Pi uptake than those with deeper root systems (Figure 5.3; Liao *et al.* 2001). Bean genotypes with shallower basal roots had superior growth in a low P field trial in Honduras (Ho *et al.* 2005). Genetic analysis of bean lines segregating for basal root shallowness showed co-segregation of QTL for root shallowness and Pi uptake in the field in Colombia (Liao *et al.* 2004). In maize, genotypes with shallower seminal roots (analogous to basal roots in dicots) had superior growth in low P soils in the field and glasshouse (Zhu *et al.* 2005b). Similar results have been observed with soybean (Zhao et al. 2004). It therefore appears that basal root shallowness is an important trait for topsoil foraging and P acquisition efficiency in annual crops.

In crops such as bean, adventitious roots emerge from the subterranean portion of the hypocotyl and grow horizontally through the topsoil. Adventitious rooting is therefore an important element of topsoil exploration by the root system. Bean genotypes differ in their extent of adventitious rooting and in the regulation of this trait by P (Miller *et al.* 2003; Ochoa *et al.* 2006). As with basal root gravitropism, genotypic and P-induced adventitious rooting vary widely, from virtually no adventitious rooting in some conditions to dozens of adventitious roots in others (Miller *et al.* 2003; Ochoa *et al.* 2006). A field study in a tropical low P soil showed that bean genotypes with greater growth and Pi uptake had more adventitious rooting relative to basal root growth than did P-inefficient genotypes (Miller *et al.* 2003). Adventitious roots may have several benefits for topsoil exploration. Obviously, their horizontal growth concentrates their foraging activity in the topsoil. Other advantages may relate to the anatomical and morphological differences between adventitious roots and basal roots. In bean, adventitious roots have greater specific

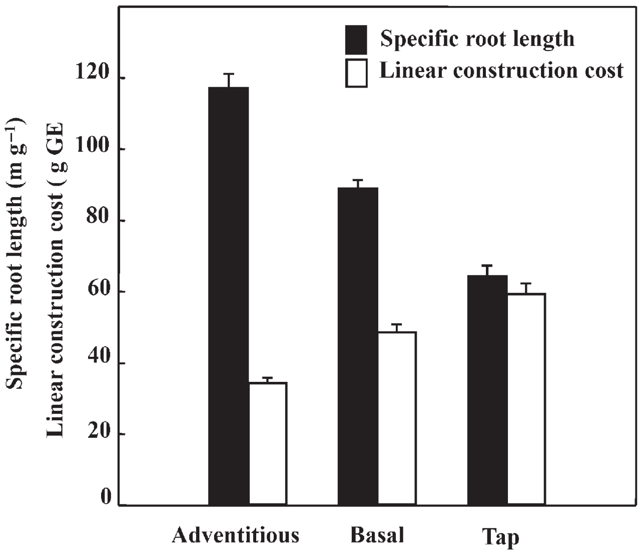

Fig. 5.4 Specific root length and linear construction cost (in glucose equivalents per cm root length) of root classes of common bean (*Phaseolus vulgaris* L.). Each bar is the mean of four replicates, error bars = SEM. (From Lynch and Ho (2005). With permission.)

root length (root length per unit root mass) than other root types (Figure 5.4). This is advantageous for topsoil exploration because it enables the plant to explore a larger volume of soil per unit of metabolic investment in root tissue (Lynch and St. Clair 2004). Also, adventitious roots may have a greater abundance of aerenchyma than other root types (Vartapetian and Jackson 1997), which may be a mechanism of reducing the metabolic costs of soil exploration (see below). Finally, adventitious roots also have less lateral branching than basal roots, which would again serve to disperse root foraging over larger soil volumes for a given metabolic investment (Miller *et al.* 2003).

Reducing root metabolic costs of soil exploration

A number of studies have shown that the metabolic costs of soil exploration by root systems (which generally include mycorrhizal symbioses) are quite substantial, and can exceed 50% of daily photosynthesis (Lambers *et al.* 2002). Following the economic paradigm of plant resource allocation (Bloom *et al.* 1985), we use the term “cost” to denote metabolic investment, including the production and maintenance of tissues, which is measurable in units of carbon (C is a convenient ‘currency’ for our analysis- other ‘currencies’, including P itself, may also be useful in some contexts; Koide and Elliott 1989; Snapp *et al.* 1995; Koide *et al.* 2000).

Plant resource allocation to root growth typically increases under nutrient stress, and therefore the metabolic costs of root growth can be a significant component of plant fitness and adaptation under nutrient stress. All else being equal, a plant that is able to acquire a limiting soil resource at reduced metabolic cost will have superior fitness, because it will have more metabolic resources available for defense, growth, and reproduction.

The importance of root C costs in plant adaptation to low P is illustrated by our work with common bean. In bean, low P availability increases the fraction of daily photosynthate respired by roots by 75% in both P-efficient and P-inefficient genotypes (Nielsen *et al.* 1998, 2001). However, P-efficient genotypes had greater root growth per unit root respiration than did P-inefficient genotypes (Figure 5.5; Nielsen *et al.* 2001), which enabled P-efficient genotypes to develop more than twice as much root biomass at low P than the P-inefficient genotypes. Phosphorus-stress slightly increased the specific respiration rate (i.e. respiration per unit biomass) of roots of the P-inefficient genotype, but halved the respiration rate of roots of the P-efficient genotype (Lynch and St. Clair 2004). Thus, adaptation to low P availability in this species is associated with the ability to explore the soil at minimal metabolic cost. We refer to the metabolic cost of P acquisition as 'P acquisition efficiency', or PAE.

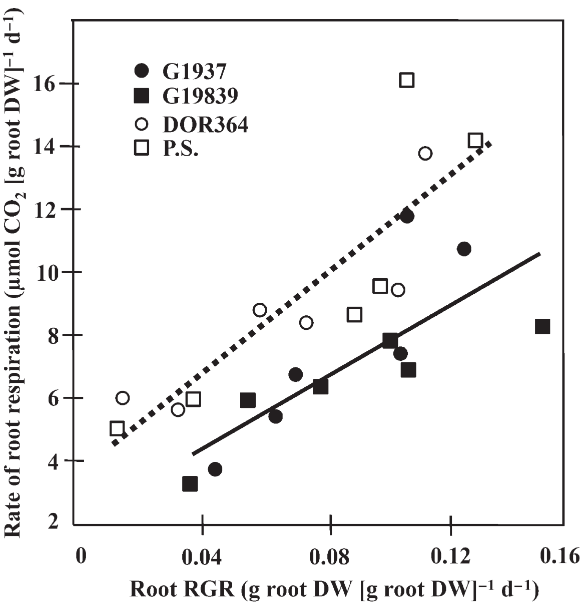

Fig. 5.5 Relationship of root respiration and root relative growth rate in four genotypes of common bean (*Phaseolus vulgaris* L.). Open symbols represent genotypes that are P-inefficient (i.e. have poor growth in low-P media), closed symbols represent genotypes that are P-efficient. (From Nielsen *et al.* (2001). With permission)

Table 5.1 Maintenance respiration dominates root respiration under low P in common bean. R_g = growth respiration, R_{iu} = ion uptake respiration, R_m = maintenance respiration. (Lynch and Ho 2005.)

		% of total root respiration		
Days after planting	Phosphorus level	R_g	R_{iu}	R_m
14	High	29	14	57
	Low	19	9	72
28	High	25	11	64
	Low	6	4	89

Several types of root traits could alter the relationship of root growth and root C cost. Geometric modeling suggests that root architecture can alter the C cost of soil exploration by regulating the extent of root competition within and among root systems (Ge *et al.* 2000; Rubio *et al.* 2001). The importance of root architecture for interplant competition for P was confirmed in field studies (Rubio *et al.* 2003). Morphological traits such as root hairs could enhance P acquisition at minimal root C cost (Bates and Lynch 2000a,b; Ma *et al.* 2001b). One mechanism of reducing root costs is to allocate more biomass to root classes that are less metabolically demanding per unit of P acquisition. We have shown that adventitious roots acquire P at less metabolic cost than basal and tap roots, and that P-stress increases relative biomass allocation to adventitious roots, especially in P-efficient genotypes (Miller *et al.* 2003).

Root respiration can be divided into three components: growth of new tissue, maintenance of existing tissue, and ion uptake and assimilation (Bouma *et al.* 1996; Amthor 2000; Lambers *et al.* 2002). As root systems mature and the proportion of non-growing tissue increases, maintenance respiration becomes an increasing fraction of total respiration. Even in young bean plants, maintenance respiration comprises 90% of total root respiration (Table 5.1). In this context it is noteworthy that a under P-stress, a P-efficient bean genotype had 50% lower maintenance respiration than a P-inefficient genotype (Ho et al. 2003; unpublished). Reduced maintenance respiration of root tissue under P-stress is an important adaptation to low P availability, by making more fixed C available for continued root growth.

Aerenchyma reduces the metabolic costs of soil exploration

Aerenchyma is a series of air spaces formed in the root cortex, and the lysigenous type, found in crop plants such as maize, is formed by a regular pattern of collapsed cortical cells (Esau 1977; Jackson and Armstrong 1999). Root aerenchyma is an adaptation to hypoxia (reviewed in Jackson and Armstrong 1999). In C3 plants, aerenchyma may also provide a photosynthetic benefit by concentrating CO_2 from root respiration and channeling it to leaf intercellular spaces (Constable and Longstreth 1994; Constable *et al.* 1992). Although the overwhelming majority of research on root aerenchyma has focused on its importance in hypoxia, root aerenchyma can also be induced by suboptimal nutrient availability. In aerated solution, aerenchyma was observed in maize roots when N, P or S were omitted from the medium (Konings and Verschuren 1980; Drew *et al.* 1989; Bouranis *et al.* 2003; Fan *et al.* 2003). The response to low P was also observed in common bean (Eshel *et al.* 1995; Fan *et al.* 2003) and rice (Lu *et al.* 1999). In maize the induction of aerenchyma by low P may be related to increased ethylene sensitivity of P-stressed roots (He *et al.* 1992).

Aerenchyma could be an important trait for plants experiencing edaphic stress, since living cortical cells are lost. This reduces root C costs by dramatically reducing maintenance respiration (Lynch and Brown 1998; Fan *et al.* 2003). Besides reducing the ongoing C cost of root maintenance, lysis of cortical cells may contribute prefixed C to root apices. An additional benefit from aerenchyma formation would be the reduced P requirement of root growth, which in conditions of P limitation can be as significant as C costs for metabolic efficiency (Snapp *et al.* 1995; Koide *et al.* 2000). Phosphorus released from cortical tissue by aerenchyma formation would be useful in meeting the P demands of new root elongation. A similar concept has been proposed for cortical senescence in grasses (Gillespie and Deacon 1988; although see Lascaris and Deacon 1991).

Results from our laboratory support the hypothesis that aerenchyma formation is a useful adaptation to low P. In bean and maize, we observed substantial genotypic variation in the induction of cortical aerenchyma by P-stress (Fan *et al.* 2003). Differences in aerenchyma formation induced by ethylene treatments and genotypic variation were correlated with proportionate reductions in root P concentration in low-P roots. Reduced P requirement for soil exploration would be advantageous in conditions of low P availability. Phosphorus liberated by senescing cortical cells could be used for continued apical growth. In low P conditions, most of the Pi taken up by roots is utilized to meet local tissue demand (Snapp and Lynch 1996). Variation in aerenchyma formation was disproportionately correlated with root respiration (Figure 5.6; Fan *et al.* 2003). Root segments with 20% cross sectional area as aerenchyma had half the respiration of roots without aerenchyma. The disproportionate effect of aerenchyma on respiration may reflect the fact that the cortical cells lost during the formation of aerenchyma are metabolically active, while inactive tissues such as sclerenchyma and xylem vessels do not contribute to maintenance respiration. Results with isolated root segments were confirmed in intact plants; whole root systems of a maize genotype with abundant aerenchyma has less root respiration per unit of root length than did a genotype with less aerenchyma (Fan *et al.* 2003). In glasshouse and field studies, the high-aerenchyma maize genotype Oh43 had greater root growth in low P soil than the low-aerenchyma genotype, W64a (Zhu *et al.* 2004; unpublished). In maize, root porosity was highly correlated with sustained root growth under low P (Figure 5.7).

Genetic variation for aerenchyma induction in response to waterlogging has been observed in many species, including banana (Aguilar *et al.* 1999), wheat (Huang *et al.* 1994), barley (Garthwaite *et al.* 2003) and maize (Lizaso *et al.* 2001; Mano *et al.* 2006). Related species may also vary in constitutive (non-stressed) aerenchyma formation (Ray *et al.* 1998; Visser *et al.* 2000; Mano *et al.* 2007). We

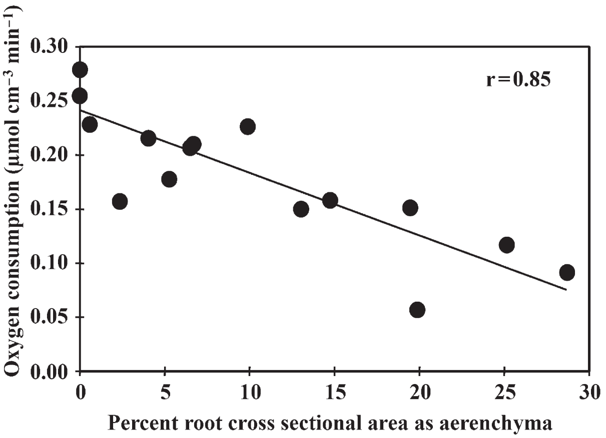

Fig. 5.6 Increasing abundance of aerenchyma is associated with reduced respiration in maize (*Zea mays* L.) roots. Each data point is the mean of 6 measurements of respiration and 10–12 measurements of aerenchyma on comparable root segments. (From Fan *et al.* (2003). with permission.)

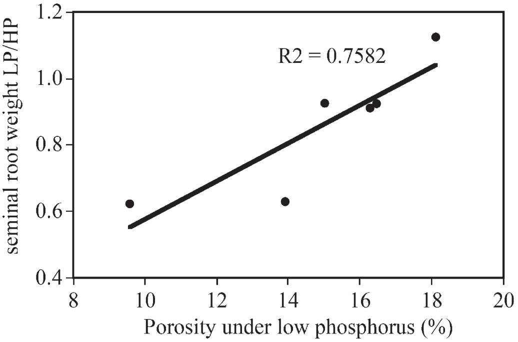

Fig. 5.7 Maintenance of root growth in a low-P field as related to cortical aerenchyma formation in unrelated maize (*Zea mays* L.) genotypes. Root weights are expressed as the proportion of corresponding high-P roots. Each point is the mean of four replicates. (Zhu, Kaeppler, and Lynch, unpublished, 2004.)

observed large genotypic variation (200–300%) in aerenchyma formation in response to P-stress in both maize and bean (Fan *et al.* 2003). Such variation raises interesting questions regarding the adaptive importance and functional tradeoffs for aerenchyma in diverse environments. Possible tradeoffs to aerenchyma formation include reduced physical resistance to crushing (Striker *et al.* 2006, 2007), reduced radial water transport (Fan *et al.* 2007), reduced mycorrhizal habitat, and increased axial spread of root pathogens. The large intraspecific variation in important crop species (Fan *et al.* 2003; Mano *et al.* 2006) also makes aerenchyma amenable to plant breeding, as is currently underway to enhance flooding tolerance in maize and other grains (Ray *et al.* 1999; Setter and Waters 2003).

Root etiolation

Shoots respond to low light intensity by etiolation, enhanced elongation at the expense of radial thickening and lateral shoot growth. This response is adaptive by increasing the likelihood of the shoot growing into better illumination and by increasing light capture in competitive situations. We hypothesize that an analogous process occurs in roots sensing low P availability.

There are many reports of increased fineness of roots under nutrient deficiency, usually described as increased specific root length (SRL, root length per unit weight). However, increased SRL could result from the increased proportion of secondary roots, since comparisons are not usually made within root classes (Eissenstat *et al*. 2000; Forde and Lorenzo 2001). Evidence for increased, reduced, or unchanged SRL can be found in the literature, but most reports do not consider variation in tissue density or variation in SRL within root classes, and are therefore not direct measurements of root diameter (Ryser and Lambers 1995; Gahoonia and Nielsen 2004). Careful studies of the effect of nutrient stress on root diameter within root classes and orders are needed to determine whether root etiolation could be an adaptive trait.

Under low P availability, root elongation is emphasized at the expense of lateral branching (Borch *et al*. 1999) and secondary growth (Eshel *et al*. 1995). There have been a few reports on increased diameter of specific root classes under high nutrient availability, including nitrate (Hackett 1972; Drew and Saker 1978; Ryser and Lambers 1995) and P (Xie and Yu 2003; Zhu and Lynch 2004). Bean basal roots show increased root diameter under high P, primarily in the older parts of the root (Figure 5.8). The larger diameter of the older parts of basal roots grown in high P was largely a result of a greater area of the stele, both in absolute area and relative to total root area (Fan *et al*. 2003). Similarly, barley roots grown with high nitrate showed an increase in stele diameter (Drew and Saker 1978), so this response is not restricted to dicots. In our study of maize genotypes with contrasting P efficiencies, we found that lateral root SRL and diameter varied among genotypes, and that smaller diameter and greater SRL of lateral roots was associated with faster lateral root growth, which in turn was associated with higher shoot growth and P efficiency (Zhu and Lynch 2004). Furthermore, there was genetic variation in plasticity of this trait, i.e. its response to P availability.

Particular root types may be more likely to alter their diameter in response to nutrient stress. In studies of barley, high nitrate increased the diameter of first and second order lateral roots, but not seminal roots (Drew and Saker 1978). In our study of primary root elongation in Arabidopsis, no difference in diameter could be discerned between high and low P treatments (Ma *et al*. 2003). Timing and extent of etiolation may vary with root class, order, and extent of the nutrient stress. ‘Root etiolation’ is presumably adaptive by reducing the metabolic costs of root extension into new soil domains that may have greater P availability. This phenomenon deserves further study.

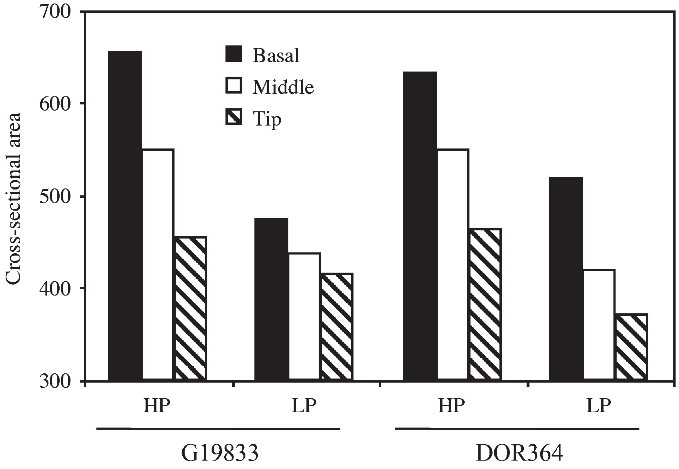

Fig. 5.8 Cross-sectional area of common bean (*Phaseolus vulgaris* L.) basal roots grown for six weeks with high (1 mM, HP) or low (1 µM, LP) phosphorus. Total cross-sectional area was measured from segments of the most basal (2 cm from point of origin), central, and apical (2 cm from root tip) portions of one basal root from each of six plants per genotype and treatment. Values shown are means, error bars = SEM. (Graph created from data in Fan *et al.* (2003). With permission.)

Like shoot etiolation, root etiolation increases exploration at the expense of mechanical strength. Finer roots may be able to penetrate smaller pores in soil, but have less ability to push soil particles aside, so roots grown in soils with high bulk density tend to have a larger diameter and reduced branching (Bennie 1991). In experiments on the effects of co-occurring soil compaction and P-deficiency, roots increased their diameter with increasing bulk density only when supplied with P (Hoffmann and Jungk 1995). Root etiolation may also have negative tradeoffs in terms of turnover rates, desiccation tolerance, susceptibility to herbivory and other characteristics (Eissenstat *et al.* 2000).

Root hairs

Root hairs are subcellular protrusions of root epidermal cells that are important for the acquisition of relatively immobile nutrients such as P (Clarkson 1985; Peterson and Farquhar 1996; Jungk 2001). Several lines of evidence indicate that root hairs contribute to Pi acquisition. First, mathematical modeling indicates that root hairs substantially increase Pi acquisition from the soil solution, by expanding the soil volume subject to Pi depletion through diffusion to the root surface (Bouldin 1961). Indirect evidence from autoradiography demonstrated that root hairs increase the size of Pi depletion zones around roots (Lewis and Quirk 1967; Bhat and Nye 1974). The inclusion of root hairs improved estimates of crop Pi uptake in simulation models (Itoh and Barber 1983a,b). More recently, direct evidence was provided for Pi uptake by root hairs (Gahoonia and Nielsen 1998).

Root hairs may also assist the dispersion of exudates such as organic acids throughout the rhizosphere, which improve P bioavailability in many soils (Hinsinger 2001; Ryan *et al.* 2001). Mutants of Arabidopsis and barley lacking root hairs have severely impaired Pi uptake (Bates and Lynch 2000a,b; Gahoonia and Nielsen 2003) and in the case of Arabidopsis, reduced competitiveness in low P soil (Bates and Lynch 2001). Both root hair length (Bates and Lynch 1996) and root hair density (Ma *et al.* 2001a) are highly regulated by P availability, which suggests that they have value to plants in low P soil. Geometric modeling indicated that responses of root hairs to P availability interact synergistically to improve P acquisition (Ma *et al.* 2001b). Variation among species in root hair length is correlated with P acquisition (Itoh and Barber 1983b; Föhse *et al.* 1991; Gahoonia *et al.* 1999), as is intraspecific variation among genotypes of white clover (Caradus 1981), barley and wheat (Gahoonia *et al.* 1997, 2001; Gahoonia and Nielsen 1997), common bean (Miguel 2004; Yan *et al.* 2004), and turfgrass (Green *et al.* 1991).

Genotypic variation in root hair length and density in maize and common bean is controlled by several major Quantitative Trait Loci (QTL; Yan *et al.* 2004; Zhu *et al.* 2005c), suggesting that this trait could be selected in crop breeding programs through marker aided selection (MAS), as well as through direct phenotypic screening. Root hairs are particularly important for P acquisition in non-mycorrhizal plants, since mycorrhizal hyphae fulfill some of the same functions as root hairs. However, genotypic variation in root hair length and density is important for PAE regardless of the mycorrhizal status of the plant (Figure 5.9; Miguel 2004). Root hairs are attractive targets for crop breeding programs because there is large genotypic variation, substantial effect of this variation on PAE (regardless of mycorrhizal status), relatively simple genetic control, and opportunities for direct phenotypic selection (Gahoonia and Nielsen 2004; Lynch 2007).

Root turnover

Root senescence, or turnover, could have positive or negative effects on the efficiency of Pi acquisition. Negative effects would result if roots were lost in fertile soil domains, resulting in loss of prior metabolic investment in those roots, as well as the opportunity costs of P that is unexploited, or worse, exploited by a competitor. Positive effects could result from the pruning of roots in infertile soil domains, thereby avoiding ongoing maintenance costs of unproductive organs, which is important, since maintenance costs rapidly overtake construction cost in most roots (e.g. Table 5.1; Peng *et al.* 1993; Nielsen *et al.* 1998). It has also been proposed that greater root turnover or "root renewal" could enhance P acquisition by increasing soil exploration and by replacing older roots with younger ones more active in Pi

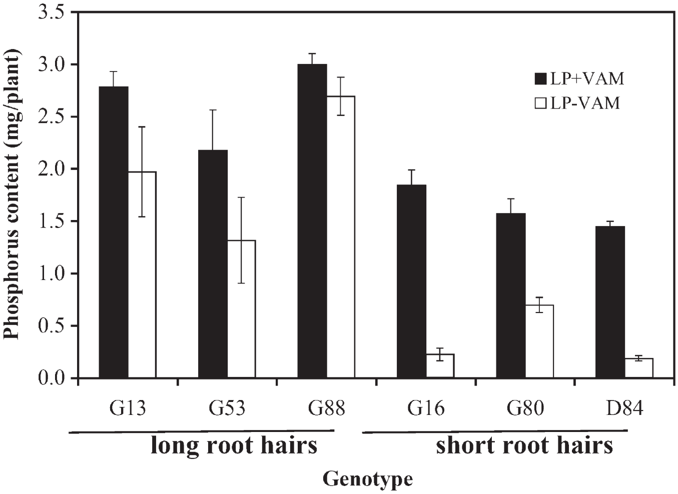

Fig. 5.9 Longer root hairs improve phosphorus acquisition in the presence and absence of mycorrhizal inoculation in common bean (*Phaseolus vulgaris* L.). Plants were grown for 28 days in low-P soil with (+VAM) or without (-VAM) mycorrhizal inoculum. Genotypes are recombinant inbred lines having long or short root hairs. Each bar is the mean of four replicates, error bars = SEM. (Miguel 2004.)

uptake (Steingrobe *et al.* 2001). Regulated senescence of roots would permit the remobilization of root resources, including carbohydrates and nutrients, to other plant activities, notably to reproductive growth in annual plants. In common bean, there is no evidence that roots in infertile soil domains are preferentially senesced (Snapp and Lynch 1996), or that programmed root senescence occurs during reproductive development (Fisher *et al.* 2002). It appears that significant root turnover observed in the field is the result of biotic and abiotic stress rather than programmed plant responses (Eissenstat and Yanai 1997; Fisher *et al.* 2002). This is supported by the observation that P availability was positively associated with soil biological activity and fine root turnover in a Hawaiian montane forest (Ostertag 2001). A report of increased root turnover with lower P availability in barley late in the season (Steingrobe *et al.* 2001) may have been confounded by P effects on phenology (see below). Therefore, traits that affect root lifespan, such as defense chemistry or tissue composition, may have only indirect effects on low P adaptation.

TARGETING P MOBILIZATION IN THE RHIZOSPHERE

Several root traits contribute to Pi acquisition by increasing the bioavailability of P in the rhizosphere. Exudation of carboxylates, such as citrate and malate, is particularly important for Pi acquisition from P-fixing soils. Deprotonated carboxylates chelate Al^{3+}, Fe^{3+} and Ca^{2+}, which results in mobilization of Pi from bound forms (Hinsinger 2001). This activity is complemented in neutral and alkaline soils by rhizosphere acidification, which results in increased solubility of Ca-phosphates (Hinsinger 2001). Although carboxylate release from roots is accentuated under P-deficiency conditions in many species, recent evidence showed that this activity is constitutive in three genotypes of chickpea (Wouterlood *et al.* 2004; Wouterlood *et al.* 2005). The subject of organic acid excretion and its importance for release of Pi from inorganic forms has been discussed extensively in several recent reviews (Hinsinger 2001; Kochian *et al.* 2004). Organic acid excretion is also important for aluminum tolerance, which is related to P efficiency traits, since excess aluminum availability coincides with P deficiency in many acid soils (Kochian *et al.* 2005). Overexpression of enzymes responsible for organic acid production in roots improves plant growth in soils with excess aluminum or low P availability (Koyama *et al.* 2000; Lopez-Bucio *et al.* 2000; Tesfaye *et al.* 2001).

Since a considerable proportion of P can occur in organic forms, plants can increase P availability in the rhizosphere by secreting phosphohydrolases to mineralize Pi from organic compounds (Marschner 1995; Abel *et al.* 2002; Vance *et al.* 2003). Secreted acid phosphatases have been shown to be upregulated under P deficiency (Marschner 1995; Vance *et al.* 2003; Tomscha *et al.* 2004). Their significance for P nutrition under P-limiting conditions has been demonstrated (Barrett-Lennard *et al.* 1993; Li *et al.* 2003, 2004; Tomscha *et al.* 2004), although their importance seems to vary with species, cropping system, and forms of organic P in the soil (Yun and Kaeppler 2001; Li *et al.* 2003, 2004; George *et al.* 2005). Exudate metabolism and production by rhizosphere microflora introduce significant complexity in the relationship between root release of exudates and the effectiveness of exudates in improving Pi acquisition by the root.

The strong interactions of root exudates with the chemical and biological characteristics of the rhizosphere highlight the important role of root architecture in placing exudates in specific soil domains. Many well-developed soils such as Spodosols, Mollisols, Andisols, Ultisols, Alfisols, and Gelisols, together comprising some 39% of the earth's ice-free land surface, have highly differentiated horizons that vary sharply in chemical, physical, and biological properties (Soil Survey Staff 1999). Phosphatases are useful for mobilization of organic phosphate esters, which are found in organic-matter rich surface horizons but, in most soils, are scarce in subsurface horizons several centimeters away. Carboxylates are especially useful in liberating Pi adsorbed to oxide surfaces, which are common in subsurface horizons but less so in the topsoil. Root architectures that deploy roots to surface or subsurface horizons should therefore have a significant impact on the functional importance of exudates for P acquisition. This largely unexplored topic is an example of trait synergy (see below).

Cluster roots

Cluster roots are zones of tightly packed, short, hairy rootlets that occur widely in Proteaceae (where they are called proteoid roots) and in several other plant families (Barber 1995; Diem *et al.* 2000; Neumann and Martinoia 2002; Lamont 2003;

Shane and Lambers 2005; Lambers *et al.* 2006). Cluster roots provide a unique mechanism for acquiring P in extremely P-poor environments by concentrating the P-mobilizing mechanisms described above into a small volume of soil. Cluster root formation and attendant secretion of organic acids, H^+ ions, and acid phosphatases are promoted by P-deficiency and in some species under other conditions such as Fe and N deficiency (Skene 2001; Neumann and Martinoia 2002; Lamont 2003; Vance *et al.* 2003).

Only a few crop species form cluster roots, notably white lupin and some Cucurbitaceae (Waters and Blevins 2000; Neumann and Martinoia 2002). While white lupin has been studied extensively, the impact of cluster roots on other crops has received little attention. One report on cucurbits implicates cluster root formation in Fe(III) reduction (Waters and Blevins 2000). We have failed to observe cluster root formation in P-stressed cucurbits (Postma and Lynch 2006; unpublished data). This adaptation may not be significant for Pi acquisition for crops other than white lupin.

The fact that so few species employ this strategy, and the Proteaceae are endemic to soils with extremely low P availability, indicates that there are significant tradeoffs to this strategy. One is that cluster roots have a high metabolic requirement. Lambers and colleagues estimate that over half of all photosynthetic carbohydrate production is required for the growth, respiration, and exudate production by cluster roots of one species (Lambers *et al.* 2006). Another potential liability to localized rhizosphere acidification is the release of toxic metals including aluminum or heavy metals. A comparison of cluster forming vs. non-cluster forming lupins showed that the cluster forming species took up more Cd, a toxic contaminant of P fertilizer sources (Brennan and Bolland 2003). The risk of metal toxicity may be one reason that cluster-rooted species are often found on sandy soils with low metal content. There may be additional tradeoffs associated with concentration of root foraging activity in limited domains, such as reduced acquisition of more mobile and dispersed nutrients, as well as water.

MYCORRHIZAL SYMBIOSES

The majority of higher plant species have mycorrhizal symbioses with fungi that assist nutrient acquisition (Smith and Read 1997). Ectomycorrhizas enhance P acquisition via mobilization of sparingly soluble P complexes, whereas both ectomycorrhizas and the vesicular-arbuscular mycorrhizas common in many annuals and hardwood species enhance Pi acquisition because they increase the volume of soil explored beyond the depletion zone surrounding the root itself. In exchange for Pi supplied to the plant, the fungal symbiont obtains reduced carbon. Therefore, the carbon cost to the plant of mycorrhizal symbioses is one component of the cost of Pi acquisition in most species. In bean, mycorrhizal colonization increased root Pi acquisition, but the resulting increase in shoot photosynthesis did not result in increased plant growth because of greater root respiration (Nielsen *et al.* 1998). At high P supply, mycorrhizal colonization reduced the growth of citrus seedlings because of greater root carbon cost (Peng *et al.* 1993). In general, the costs of the mycorrhizal symbiosis in various herbaceous and woody species ranges from 4% to 20% of daily net photosynthesis (Koch and Johnson 1984; Harris and Paul 1987; Douds *et al.* 1988; Jakobsen and Rosendahl 1990; Eissenstat *et al.* 1993; Nielsen *et al.* 1998). The greater metabolic burden of mycorrhizal roots may contribute to the non-beneficial or even parasitic role that mycorrhizal fungi play in agroecosystems (Ryan and Graham 2002).

Mycorrhizal symbioses have attracted a great deal of attention by researchers in the past 30 years. The importance of mycorrhizal symbioses for Pi acquisition has led some mycorrhizal researchers to the belief that root traits are secondary or trivial in importance for Pi acquisition compared to fungal-assisted Pi acquisition (Smith *et al.* 2003). In this context it is useful to consider the strong correlations observed between Pi uptake and root traits such as root hair length (Figure 5.10; Miguel 2004; see also references cited above) and root shallowness (Lynch and Brown 2001) even in the presence of mycorrhizas. This could signify that mycorrhizal foraging is incomplete and can be supplemented by direct root foraging. Alternatively, extraradical hyphae could be restricted to the volume of soil near the root (Owusu-Bennoah *et al.* 2002), so that root architectural patterns have a strong influence on foraging patterns by the fungal symbiont. In our research with maize, soybean, and common bean, we have observed similar genotypic rankings for plant growth in low P soil in the field where mycorrhizas are formed and in controlled environments without mycorrhizas (Bonser *et al.* 1996; Miguel 2004; Ho *et al.* 2005). This suggests that for these annual crops, mycorrhizal symbiosis changes the effective fertility status of the soil environment but does not represent a selection criterion (either through natural selection or in plant breeding) among genotypes, possibly because it is ubiquitous.

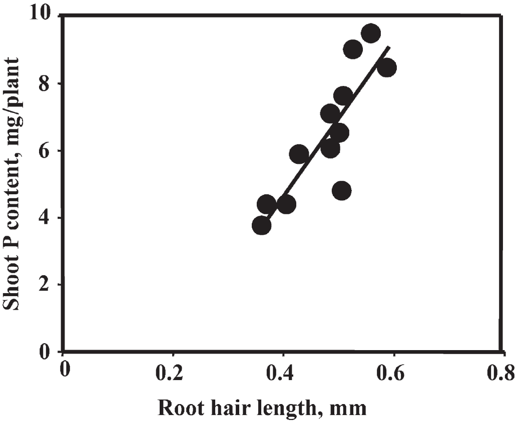

Fig. 5.10 Effect of root hair length on phosphorus content of common bean (*Phaseolus vulgaris* L.) genotypes. Plants were grown for 35 days in low-P soil in the field in Costa Rica. Each point is the mean of four replicates of one genotype; the set of genotypes are six recombinant inbred lines having long or short root hairs. (Miguel 2004)

PHENOLOGY

Some annual plants respond to P stress by delayed maturation (Rossiter 1978; Chauhan *et al*. 1992; Ma *et al*. 2002). This could be adaptive for P acquisition by permitting continued root growth, and by extending the period of time in which existing roots acquire Pi. Time is particularly important for Pi acquisition, since Pi diffusion through soil is slow, as is recharge of P-depleted soil (Tinker and Nye 2000). We call this phenomenon 'root foraging duration' by analogy with leaf area duration. We have observed that root foraging duration (the integral of root length over time) is highly correlated with Pi acquisition in Arabidopsis genotypes of contrasting phenology (Figure 5.11). In addition to possible benefits for Pi acquisition, an extended growing season would also increase the metabolic utility of acquired P, for example by extending the time leaf P could be employed to generate photosynthates. In other words, the utility of P to the plant is dependent on the length of time the P is used by the plant, which in general would be greater with an extended growing season. Phenology is responsive to P availability in some plants and there is a range of maturities available within crop species. If it is demonstrated that delayed maturation is a positive adaptation to low P availability, genotypic variation for this trait may have value in crop breeding programs, especially in tropical agroecosystems where temperature and moisture availability do not limit the effective growing season.

TRAIT SYNERGY

Several root strategies for Pi acquisition may have functional interactions with each other or with other plant traits. These interactions could be positive or synergistic in improving P efficiency traits, or they may be antagonistic. An example of trait

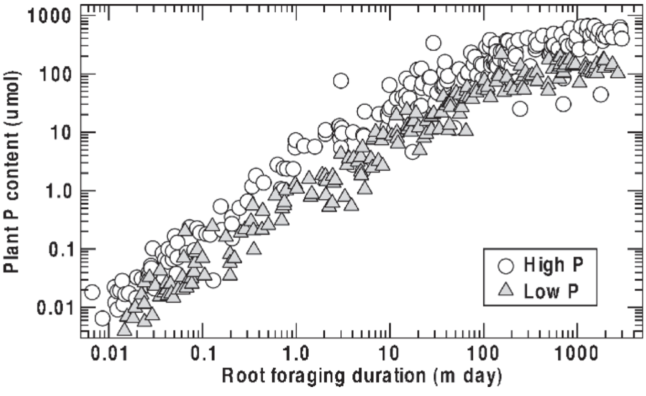

Fig. 5.11 Plant phosphorus content and root foraging duration for seven genotypes of *Arabidopsis thaliana* grown in soils with high and low phosphorus availability. Total phosphorus acquired is strongly correlated with root foraging duration, with plants grown in high phosphorus soil acquiring more phosphorus at a given level of root foraging duration. (Nord and Lynch, unpublished, 2007)

synergy in Pi acquisition is the interaction of four distinct root hair traits; root hair length, root hair density, the distance from the root tip to the first appearance of root hairs, and the pattern of root hair bearing epidermal cells (trichoblasts) among non hair bearing cells (atrichoblasts). Low P availability causes coordinated increases in root hair length and density in many species (Brewster *et al.* 1976; Foehse and Jungk 1983; Bates and Lynch 1996; Ma *et al.* 2001a). In Arabidopsis, low P availability also shortens the distance from the first root hair to the root tip, and changes the geometry of trichoblasts by increasing the number of trichoblast files, caused by cortical reorganization (Ma *et al.* 2001a, 2003). Geometric modeling showed that the combined effect of these four traits on Pi acquisition was 371% greater than their additive effects, demonstrating substantial morphological synergy (Ma *et al.* 2001b). Synergism among root hair traits may account for their coordinated regulation.

Traits of individual root axes such as root hairs and root exudates may have synergism with root architectural traits, which locate root axes in soil domains with varying P availability. For example, longer root hairs would be expected to provide greater benefit to the plant if they were positioned in P-replete topsoil as opposed to P-deficient subsoil. Phosphatases that mobilize Pi from soil organic matter would be more useful if exuded by shallow roots than by deep roots, since in most soils organic matter decreases with depth. In contrast, organic acids that mobilize Pi from Fe and Al oxides may be more useful when released into deeper soil horizons where these forms of P predominate. Root architectural traits may themselves display interactions, by altering the extent of inter-root competition, which is an important component of overall root foraging efficiency (Ge *et al.* 2000; Rubio *et al.* 2001, 2003). For example, root systems combining deep rooting (through, for example, lateral branching from the deeper parts of the primary and basal roots) with shallow rooting (through adventitious roots or shallow basal roots) would be expected to be more complementary than root systems in which distinct root classes competed for the same soil niche (Walk *et al.* 2006). This is especially relevant in the context of drought, since in many environments water is a deep soil resource while P is a shallow resource (see discussion below). We know very little about the interaction of traits related to P acquisition, despite the importance of trait interactions for whole plant performance. This is pertinent to plant breeding, since traits under distinct genetic control could be combined to maximize positive synergy.

TRADEOFFS

The utility of a trait for plants in low P environments must take into account potential tradeoffs of the trait for other plant processes. The most obvious tradeoff for many traits is simply the opportunity cost resulting from diversion of plant resources from other functions. For example, the production of adventitious roots reduces the development of basal roots, which in certain soils can be detrimental to overall plant P acquisition (Walk *et al.* 2006). Since soil resource distribution is heterogeneous, architectural tradeoffs can also occur when the exploitation of one soil domain reduces exploitation of another soil domain with its attendant resources.

An important tradeoff or opportunity cost to topsoil foraging is increased sensitivity to drought stress, since water is a deep soil resource in many environments. A comparison of deep-rooted and shallow-rooted bean genotypes showed that while shallower genotypes had superior growth under P stress, deep-rooted genotypes had superior growth under water stress (Figure 5.12; Ho *et al.* 2005). These results are consistent with economic optimization modeling of the relationship between root architecture and multiple resource acquisition, particularly water and P (Ho *et al.* 2004). The general solution of the model states that a plant will locate its roots at a soil depth where the marginal benefit of water and P acquisition will exactly equal the marginal cost of inter-root competition (Ho *et al.* 2004). Indeed, bean genotypes that are best adapted to low P environments, where P is localized in the surface soil, tend to have a shallower basal root angle, whereas genotypes that are adapted to terminal drought environments have deeper root systems (Ho *et al.* 2005). This example illustrates the importance of considering tradeoffs in assessing the adaptive importance of specific root traits, especially in crop breeding for distinct environments.

The large genotypic variation for root traits that appear to be positive adaptations for nutrient acquisition may be caused or maintained by tradeoffs incurred by certain phenotypes. For example, long, dense root hairs improve Pi acquisition at minimal metabolic cost (see references above), yet a large proportion of crop genotypes have few, sparse root hairs, and many genotypes display plasticity in root hair traits, so that under high fertility, root hairs are suppressed. This could suggest that there are potential costs to root hairs, such as increased susceptibility to root pathogens. Similarly, cortical aerenchyma appears to reduce the metabolic costs of soil exploration (see references above), yet substantial intraspecific variation for constitutive aerenchyma formation exists, and aerenchyma formation is suppressed under high fertility. This suggests that there are potential costs to aerenchyma formation, such as reduced radial transport of water (Fan *et al.* 2007) and nutrients, or reduced mycorrhizal habitat. Such questions are largely unresolved.

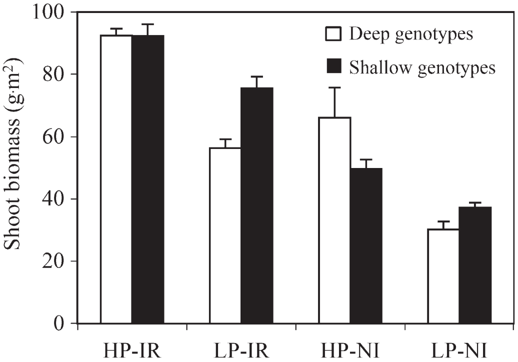

Fig. 5.12 Shoot biomass at 44 days after planting for three shallow-rooted and three deep-rooted common bean (*Phaseolus vulgaris* L.) genotypes in the field. HP = high phosphorus availability, LP = low phosphorus availability, IR = irrigated, NI = non-irrigated. Each bar is the mean of four replicates, error bars = SEM. (From Ho *et al.* (2005). With permission)

RESPONSES TO HETEROGENEOUS P AVAILABILITY

In addition to the variability in P availability with soil depth (discussed above), P availability may be heterogeneous in space and time as a result of organic matter decomposition, variation in soil composition, competition with the same or other root systems, water availability, temperature, etc. (Jackson and Caldwell 1993). Many plants have the ability to respond to these patches of higher nutrient availability in ways that are expected to increase their ability to compete for these nutrients. The responses of root systems to heterogeneous nutrient distribution have been reviewed recently (Hodge 2004), so this topic will be discussed here only in the context of agroecology.

When P-stressed plants encounter a patch of higher P availability, one advantageous response is to proliferate roots to enhance Pi acquisition from the patch. Root proliferation has been observed in nutrient patches and includes increased number, length, and branching of lateral roots. The extent to which this occurs varies among species, some showing very dramatic effects (e.g. barley; Drew 1975), while others show little or no response (Campbell *et al*. 1991; Farley and Fitter 1999). To complicate matters further, plants may alter root development in nutrient patches when roots of another plant (even of the same species) are competing within the patch (Robinson *et al*. 1999; Gersani *et al*. 2001; Maina *et al*. 2002). The available data justifies the conclusion that root proliferation in nutrient patches is likely to be useful for plants grown in intercrop systems, as is the case for many crops grown in poor soils in the tropics and subtropics.

INTERPLANT COMPETITION

The utility of traits for P efficiency will be most evident in competitive environments, including those experienced by wild plants, crops in subsistence agroecosystems, and in the high-density genetic monocultures typical of commercial agriculture. Traits influencing P efficiency will affect plant productivity, and thereby competitive performance, under P-stress. An example of this is the positive effect of root hairs on plant performance in mixed stands of Arabidopsis at low P but not at high P (Bates and Lynch 2001). Traits influencing Pi acquisition can directly affect interplant competition by removing soil P that could be accessed by competitors. For example, bean genotypes with shallow basal roots out-compete genotypes with deep basal roots in low P fields (Rubio *et al*. 2003), because of enhanced topsoil exploitation and reduced competition among roots of the same plant (Rubio *et al*. 2001).

At the population level, competition among root systems can be important in determining the utility of root traits for P efficiency. This appears to be the case for plasticity of basal root shallowness, for which genetic variation exists, i.e. some genotypes respond to P-stress by becoming more shallow, whereas others are unaffected or become deeper (Bonser *et al*. 1996; Ho *et al*. 2004, 2005). Plasticity

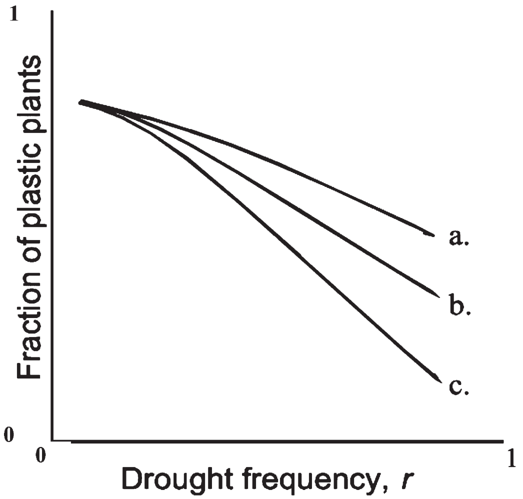

Fig. 5.13 The theoretical relationship of the equilibrium steady-state fraction of plastic plants in a population and drought frequency, where spatial competition is considered, under (a) low, (b) intermediate or (c) high drought intensity. Plastic plants in this model respond to low P availability by increasing topsoil foraging, which incurs costs in conditions of terminal drought, and when neighboring individuals have the same phenotype. (Ho 2004)

of root shallowness would generally be considered a useful trait, since plasticity would permit a plant to modify its root architecture to adapt to the prevailing edaphic stress. However, if all plants in a population were equally plastic, and therefore had the same root architecture, greater interplant competition would occur than if distinct root phenotypes existed in a population, thereby permitting complementary exploitation of distinct soil domains. Theoretical modeling showed that interplant competition could be important in determining an optimal balance of plastic and non-plastic root phenotypes under conditions of P-stress and combined P and water stress (Figure 5.13; Ho 2004). This suggests that genetic mixtures or multilines may have better performance in low P agroecosystems than genetic monocultures, especially in drought-prone environments.

ECOSYSTEM ISSUES

A better understanding of plant adaptations to P-stress is critically needed for two of the greatest challenges facing humanity in the 21st century: eliminating world hunger and understanding how natural and managed ecosystems will respond to global climate change.

The development of crops with superior growth in low P soil and with better responsiveness to applied P inputs would have tremendous value in many developing countries, where yields are limited by low soil fertility and fertilizer use is minimal (World Bank 2004). Since genotypic variation for PAE is much larger than variation for P use efficiency in crop plants, development of P-efficient crops is likely to have a great impact on agricultural productivity in these agroecosystems (Lynch and Beebe 1995). Although such genotypes would extract more P from the soil than conventional genotypes, they may actually enhance soil fertility in the

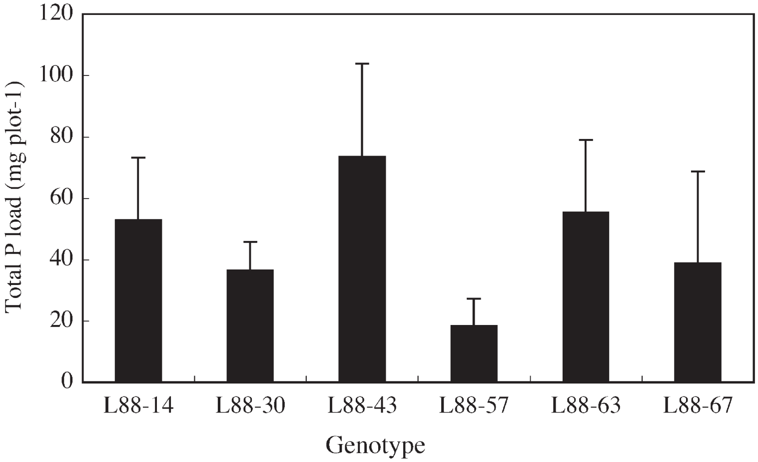

Fig. 5.14 Effect of genotype on phosphorus runoff from an unfertilized on-farm site in Costa Rica during one growing season. Beans were planted at densities typical of local practice. (Henry and Lynch, unpublished, 2007)

long term through beneficial effects on soil erosion and nutrient cycling, as well as benefits they accrue to farm income and thereby the use of fertility amendments (Lynch and Deikman 1998). For example, P runoff from common bean plots in a farmer's unfertilized field varied substantially among genotypes (Figure 5.14; Henry and Lynch 2007; unpublished).

Several genetic traits have been identified with potential utility in breeding P efficient crops, as discussed above, including root exudates, root hair traits, cortical aerenchyma, topsoil foraging through basal or adventitious rooting, and the use of multiline mixtures of root phenotypes. Deployment of these traits through plant breeding programs is resulting in progress in several crops including common bean (CIAT 1999) and soybean (Yan 2005). The success of this effort would constitute a second 'Green Revolution', benefiting the resource-poor farmers who were largely left behind by the first Green Revolution, and who represent the single largest human labor occupation (Lynch and Deikman 1998). A better understanding of the biology of traits associated with P efficiency, especially how these traits combine and their tradeoffs in specific production environments, is needed to guide plant breeding efforts.

We will not be able to understand or manage ecosystem responses to global change unless we learn more about how global change variables such as CO_2, temperature, and ozone interact with the edaphic stresses prevalent in most terrestrial ecosystems (Lynch and St. Clair 2004). The vast majority of research on plant response to global change has focused on leaf responses and has not considered edaphic stresses other than water and possibly nitrogen with any rigor, despite the fact that plant responses to edaphic stresses are primary limitations to plant productivity in most forests and managed systems. Plants limited by low soil P availability may respond to elevated CO_2 by producing more exudates and by altered root growth and architecture, which may partially alleviate P stress, but interactions with other global change variables such as drought are likely to be detrimental, as discussed above. This topic merits research.

CONCLUSIONS

Low soil P availability is a primary constraint to plant growth on earth. Accordingly, plants express a wide array of root strategies that improve Pi acquisition, including increased biomass allocation to roots and to specific root classes within the root system, root architectural traits that enhance topsoil foraging, including basal root gravitropism, adventitious rooting, and lateral root branching, reduced metabolic costs of soil exploration, via formation of cortical aerenchyma, the formation of finer roots and possibly root etiolation, root hairs, P-solubilizing root exudates, mycorrhizal symbioses, phenological plasticity, and morphological plasticity. Ecological tradeoffs and interactions among these traits are poorly understood but are likely to be important in determining the functional utility of these traits, especially in competitive environments. A better understanding of these traits is needed to guide the development of more P efficient crops for developing nations, and to understand how ecosystems will respond to global climate change.

REFERENCES

Abel S, Ticconi CA, Delatorre CA (2002) Phosphate sensing in higher plants. Physiol Plant 115: 1–8

Abelson PH (1999) A potential phosphate crisis. Science 283: 2015–2015

Aguilar EA, Turner DW, Sivasithamparam K (1999) Aerenchyma formation in roots of four banana (*Musa* spp.) cultivars. Sci Hort 80: 57–72

Al-Ghazi Y, Muller B, Pinloche S, Tranbarger TJ, Nacry P, Rossignol M, Tardieu F, Doumas P (2003) Temporal responses of Arabidopsis root architecture to phosphate starvation: evidence for the involvement of auxin signalling. Plant Cell Environ 26: 1053–1066

Amthor JS (2000) The McCree-de Wit-Penning de Vries-Thornley respiration paradigms: 30 years later. Ann Bot 86: 1–20

Anderson G (1980) Assessing organic phosphorus in soils. In: Khasawneh, FE, Sample EC, Kamprath EJ (eds), The Role of Phosphorus in Agriculture. ASA/CSSA/SSSA, Madison, WI, pp 263–310

Barber S (1962) A diffusion and mass flow concept of nutrient availability. Soil Sci 93: 39–49

Barber SA (1995) Soil Nutrient Bioavailability: A Mechanistic Approach. Wiley, New York

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

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

Bates TR, Lynch JP (2000a) Plant growth and phosphorus accumulation of wild type and two root hair mutants of *Arabidopsis thaliana* (Brassicaceae). Am J Bot 87: 958–963

Bates TR, Lynch JP (2000b) The efficiency of *Arabidopsis thaliana* (Brassicaceae) root hairs in phosphorus acquisition. Am J Bot 87: 964–970

Bates TR, Lynch JP (2001) Root hairs confer a competitive advantage under low phosphorus availability. Plant Soil 236: 243–250

Bennie A (1991) Growth and mechanical impedance. In: Waisel Y, Eshel A, Kafkafi U (eds), Plant Roots: The Hidden Half. Marcel Dekker, New York, pp 393–414

Bhat KKS, Nye PH (1974) Diffusion of phosphate to plant roots in soil III. Depletion around onion roots without root hairs. Plant Soil 41: 383–394

Bloom A, Chapin F, Mooney H (1985) Resource limitation in plants - an economic analogy. Ann Rev Ecol Syst 16: 363–392

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

Borch K, Bouma TJ, Lynch JP, Brown KM (1999) Ethylene: a regulator of root architectural responses to soil phosphorus availability. Plant Cell Environ 22: 425–431

Bouldin D (1961) Mathematical description of diffusion process in the soil. Soil Sci Soc Am Proc 25: 476–480

Bouma TJ, Broekhuysen AGM, Veen BW (1996) Analysis of root respiration of *Solanum tuberosum* as related to growth, ion uptake and maintenance of biomass. Plant Physiol Biochem 34: 795–806

Bouranis DL, Chorianopoulou SN, Siyiannis VF, Protonotarios VE, Hawkesford MJ (2003) Aerenchyma formation in roots of maize during sulphate starvation. Planta 217: 382–391

Brennan RF, Bolland MDA (2003) *Lupinus luteus* cv. Wodjil takes up more phosphorus and cadmium than *Lupinus angustifolius* cv. Kalya. Plant Soil 248: 167–185

Brewster J, Bhat K, Nye P (1976) The possibility of predicting solute uptake and plant growth response from independently measured soil and plant characteristics. IV. The growth and uptake of rape in solutions of different phosphorus concentrations. Plant Soil 44: 279–293

Campbell BD, Grime JP, Mackey JML (1991) A trade-off between scale and precision in resource foraging. Oecologia 87: 532–538

Caradus J (1981) Effect of root hair length on white clover growth over a range of soil phosphorus levels. New Zeal J Agr Res 24: 359–364

Chauhan YS, Johansen C, Venkataratnam N (1992) Effects of phosphorus deficiency on phenology and yield components of short-duration pigeonpea. Trop Agr 69: 235–238

Chu W, Chang S (1966) Surface activity of inorganic soil phosphorus. Soil Sci 101: 459–464

CIAT (1999) Bean Project 1998 Annual Report. CIAT, Cali, Colombia

Clarkson D (1985) Factors affecting mineral nutrient acquisition by plants. Ann Rev Plant Physiol 36: 77–115

Comerford N (1998) Soil phosphorus bioavailability. In: Lynch J, Deikman J (eds), Phosphorus in Plant Biology: Regulatory Roles in Molecular, Cellular, Organismic, and Ecosystem Processes. ASPP, Rockville, MD, pp 136–147

Constable J, Longstreth DJ (1994) Aerenchyma carbon dioxide can be assimilated in *Typha latifolia* L. leaves. Plant Physiol 106: 1065–1072

Constable JVH, Grace JB, Longstreth DJ (1992) High carbon dioxide concentrations in aerenchyma of *Typha latifolia*. Am J Bot 79: 415–418

Diem HG, Duhoux E, Zaid H, Arahou M (2000) Cluster roots in Casuarinaceae: role and relationship to soil nutrient factors. Ann Bot 85: 929–936

Douds DD, Johnson CR, Koch KE (1988) Carbon cost of the fungal symbiont relative to net leaf-P accumulation in a split-root VA mycorrhizal symbiosis. Plant Physiol 86: 491–496

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

Drew M, He C, Morgan P (1989) Decreased ethylene biosynthesis, and induction of aerenchyma, by nitrogen- or phosphate-starvation in adventitious roots of *Zea mays* L. Plant Physiol 91: 266–271

Drew MC, Saker LR (1978) Nutrient supply and the growth of the seminal root system in barley. J Exp Bot 29: 435–451

Eissenstat DM, Yanai RD (1997) The ecology of root lifespan. Adv Ecol Res 27: 1–60

Eissenstat DM, Graham JH, Syvertsen JP, Drouillard DL (1993) Carbon economy of sour orange in relation to mycorrhizal colonization and phosphorus status. Ann Bot 71: 1–10

Eissenstat DM, Wells CE, Yanai RD, Whitbeck JL (2000) Building roots in a changing environment: implications for root longevity. New Phytol 147: 33–42

Esau K (1977) Anatomy of Seed Plants. Wiley, New York

Eshel A, Nielsen K, Lynch J (1995) Response of bean root systems to low level of P. In: Plant Roots - From Cells to Systems. 14th Long Ashton International Symposium. IACR-Long Ashton Research Station, Bristol, UK

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

Fan M, Bai R, Zhao X, Zhang J (2007) Aerenchyma formed under phosphorus deficiency contributes to the reduced root hydraulic conductivity in maize roots. J Integr Plant Biol 49: 598–604

Farley RA, Fitter AH (1999) The responses of seven co-occurring woodland herbaceous perennials to localized nutrient-rich patches. J Ecol 87: 849–859

Fisher MCT, Eissenstat DM, Lynch JP (2002) Lack of evidence for programmed root senescence in common bean (*Phaseolus vulgaris*) grown at different levels of phosphorus supply. New Phytol 153: 63–71

Foehse D, Jungk A (1983) Influence of phosphate and nitrate supply on root hair formation of rape, spinach and tomato plants. Plant Soil 74: 359–368

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

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

Gahoonia TS, Nielsen NE (1998) Direct evidence on participation of root hairs in phosphorus (^{32}P) uptake from soil. Plant Soil 198: 147–152

Gahoonia TS, Nielsen NE (2003) Phosphorus (P) uptake and growth of a root hairless barley mutant (bald root barley, *brb*) and wild type in low- and high-P soils. Plant Cell Environ 26: 1759–1766

Gahoonia TS, Nielsen NE (2004) Root traits as tools for creating phosphorus efficient crop varieties. Plant Soil 260: 47–57

Gahoonia TS, Care D, Nielsen NE (1997) Root hairs and phosphorus acquisition of wheat and barley cultivars. Plant Soil 191: 181–188

Gahoonia TS, Nielsen NE, Lyshede OB (1999) Phosphorus (P) acquisition of cereal cultivars in the field at three levels of P fertilization. Plant Soil 211: 269–281

Gahoonia TS, Nielsen NE, Joshi PA, Jahoor A (2001) A root hairless barley mutant for elucidating genetic of root hairs and phosphorus uptake. Plant Soil 235: 211–219

Garthwaite AJ, von Bothmer R, Colmer TD (2003) Diversity in root aeration traits associated with waterlogging tolerance in the genus *Hordeum*. Funct Plant Biol 30: 875–889

Ge Z, Rubio G, Lynch JP (2000) The importance of root gravitropism for inter-root competition and phosphorus acquisition efficiency: results from a geometric simulation model. Plant Soil 218: 159–171

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

Gersani M, Brown JS, O'Brien EE, Maina GM, Abramsky Z (2001) Tragedy of the commons as a result of root competition. J Ecol 89: 660–669

Gillespie IMM, Deacon JW (1988) Effects of mineral nutrients on senescence of the cortex of wheat roots and root pieces. Soil Biol Biochem 20: 525–531

Green RL, Beard JB, Oprisko MJ (1991) Root hairs and root lengths in nine warm-season turfgrass genotypes. J Am Soc Hortic Sci 116: 965–969

Gutschick V (1993) Nutrient-limited growth rates: roles of nutrient-use efficiency and of adaptations to increase uptake rate. J Exp Bot 44: 41–51

Hackett C (1972) A method of applying nutrients locally to roots under controlled conditions, and some morphological effects of locally applied nitrate on the branching of wheat roots. Aust J Biol Sci 25: 1169–1180

Halsted M, Lynch J (1996) Phosphorus responses of C-3 and C-4 species. J Exp Bot 47: 497–505

Hansen CW, Lynch J, Ottosen CO (1998) Response to phosphorus availability during vegetative and reproductive growth of chrysanthemum: I. Whole-plant carbon dioxide exchange. J Am Soc Hortic Sci 123: 215–222

Harris D, Paul E (1987) Carbon requirements of vesicular-arbuscular mycorrhizae. In: Safir GR (ed), Ecophysiology of VA Mycorrhizae. CRC, Boca Raton, FL, pp 93–105

Harrison MJ (1999) Molecular and cellular aspects of the arbuscular mycorrhizal symbiosis. Annu Rev Plant Physiol Plant Mol Biol 50: 361–389

Hartemink AE (2003) Soil Fertility Decline in the Tropics. CABI, Wageningen, The Netherlands

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

He CJ, Morgan PW, Drew MC (1992) Enhanced sensitivity to ethylene in nitrogen-starved or phosphate-starved roots of *Zea mays* l. During aerenchyma formation. Plant Physiol 98: 137–142

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

Hinsinger P, Plassard C, Tang CX, Jaillard B (2003) Origins of root-mediated pH changes in the rhizosphere and their responses to environmental constraints: a review. Plant Soil 248: 43–59

Hinsinger P, Gobran GR, Gregory PJ, Wenzel WW (2005) Rhizosphere geometry and heterogeneity arising from root mediated physical and chemical processes. New Phytol 168: 293–303

Ho MD (2004) Effects of root architecture, plasticity, and tradeoffs on water and phosphorus acquisition in heterogeneous environments. Dissertation, Penn State University

Ho MD, McCannon BC, Lynch JP (2004) Optimization modeling of plant root architecture for water and phosphorus acquisition. J Theor Biol 226: 331–340

Ho M, Rosas J, Brown K, Lynch J (2005) Root architectural tradeoffs for water and phosphorus acquisition. Funct Plant Biol 32: 737–748

Hodge A (2004) The plastic plant: root responses to heterogeneous supplies of nutrients. New Phytol 162: 9–24

Hoffmann C, Jungk A (1995) Growth and phosphorus supply of sugar-beet as affected by soil compaction and water tension. Plant Soil 176: 15–25

Huang BR, Johnson JW, Nesmith DS, Bridges DC (1994) Root and shoot growth of wheat genotypes in response to hypoxia and subsequent resumption of aeration. Crop Sci 34: 1538–1544

Itoh S, Barber SA (1983a) A numerical solution of whole plant nutrient uptake for soil root systems with root hairs. Plant Soil 70: 403–413

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

Jackson MB, Armstrong W (1999) Formation of aerenchyma and the processes of plant ventilation in relation to soil flooding and submergence. Plant Biol 1: 274–287

Jackson RB, Caldwell MM (1993) The scale of nutrient heterogeneity around individual plants and its quantification with geostatistics. Ecology 74: 612–614

Jakobsen I, Rosendahl L (1990) Carbon flow into soil and external hyphae from roots of mycorrhizal cucumber plants. New Phytol 115: 77–83

Jeschke WD, Holobrada M, Hartung W (1997) Growth of *Zea mays* l. Plants with their seminal roots only. Effects on plant development, xylem transport, mineral nutrition and the flow and distribution of abscisic acid (ABA) as a possible shoot- to-root signal. J Exp Bot 48: 1229–1239

Joner EJ, Magid J, Gahoonia TS, Jakobsen I (1995) P depletion and activity of phosphatases in the rhizosphere of mycorrhizal and nonmycorrhizal cucumber (*Cucumis sativus* L). Soil Biol Biochem 27: 1145–1151

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

Jungk A (2001) Root hairs and the acquisition of plant nutrients from soil. J Plant Nutr Soil Sci 164: 121–129

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

Koch KE, Johnson CR (1984) Photosynthate partitioning in split root citrus seedlings with mycorrhizal and non-mycorrhizal root systems. Plant Physiol 75: 26–30

Kochian LV, Hoekenga OA, Piñeros MA (2004) How do crop plants tolerate acid soils? Mechanisms of aluminum tolerance and phosphorus efficiency. Annu Rev Plant Biol 55: 459–493

Kochian LV, Piñeros MA, Hoekenga OA (2005) The physiology, genetics and molecular biology of plant aluminum resistance and toxicity. Plant Soil 274: 175–195

Koide R, Elliott G (1989) Cost, benefit and efficiency of the vesicular-arbuscular mycorrhizal symbiosis. Funct Ecol 3: 252–255

Koide RT, Goff MD, Dickie IA (2000) Component growth efficiencies of mycorrhizal and nonmycorrhizal plants. New Phytol 148: 163–168

Konings H, Verschuren G (1980) Formation of aerenchyma in roots of *Zea mays* in aerated solutions, and its relation to nutrient supply. Physiol Plant 49: 265–279

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

Lambers H, Atkin O, Millenaar FF (2002) Respiratory patterns in roots in relation to their functioning. In: Waisel Y, Eshel A, Kafkaki K (eds), Plant Roots: The Hidden Half. Marcel Dekker, New York, pp 521–552

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

Lascaris D, Deacon JW (1991) Relationship between root cortical senescence and growth of wheat as influenced by mineral nutrition, *Idriella bolleyi* (sprague) von Arx and pruning of leaves. New Phytol 118: 391–396

Lewis DG, Quirk JP (1967) Phosphate diffusion in soil and uptake by plants. Plant Soil 26: 445–453

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

Li SM, Li L, Zhang F, Tang C (2004) Acid phosphatase role in chickpea/maize intercropping. Ann Bot 94: 297–303

Liao H, Rubio G, Yan XL, Cao AQ, Brown KM, Lynch JP (2001) Effect of phosphorus availability on basal root shallowness in common bean. Plant Soil 232: 69–79

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

Lizaso JI, Melendez LM, Ramirez R (2001) Early flooding of two cultivars of tropical maize. I. Shoot and root growth. J Plant Nutr 24: 979–995

Lopez-Bucio J, Nieto-Jacobo MF, Ramirez-Rodriguez V, Herrera-Estrella L (2000) Organic acid metabolism in plants: from adaptive physiology to transgenic varieties for cultivation in extreme soils. Plant Sci 160: 1–13

Lopez-Bucio J, Hernandez-Abreu E, Sánchez-Calderon 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

Lu Y, Wassmann R, Neue HU, Huang C (1999) Impact of phosphorus supply on root exudation, aerenchyma formation and methane emission of rice plants. Biogeochemistry 47: 203–218

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

Lynch J (2005) Root architecture and nutrient acquisition. In: BassiriRad H (ed), Nutrient Acquisition by Plants. An Ecological Perspective. Springer, Berlin/Heidelberg/New York, pp 147–184

Lynch J (2007) Roots of the second green revolution. Aust J Bot 55: 493–512

Lynch JP, Beebe SE (1995) Adaptation of beans (*Phaseolus vulgaris* L.) to low phosphorus availability. HortScience 30: 1165–1171

Lynch J, Brown K (1998) Root architecture and phosphorus acquisition efficiency in common bean. In: Lynch J, Deikman J (eds), Phosphorus in Plant Biology: Regulatory Roles in Molecular, Cellular, Organismic, and Ecosystem Processes. ASPP, Rockville, MD, pp 148–156

Lynch JP, Brown KM (2001) Topsoil foraging - an architectural adaptation of plants to low phosphorus availability. Plant Soil 237: 225–237

Lynch J, Brown K (2006) Whole plant adaptations to low phosphorus availability. In: Huang B (ed), Plant-Environment Interactions (3rd edition). Taylor & Francis, New York, pp 209–242

Lynch J, Deikman J (1998) Phosphorus in Plant Biology: Regulatory Roles in Molecular, Cellular, Organismic, and Ecosystem Processes. ASPP, Rockville, MD

Lynch JP, Ho MD (2005) Rhizoeconomics: carbon costs of phosphorus acquisition. Plant Soil 269: 45–56

Lynch JP, St. Clair SB (2004) Mineral stress: the missing link in understanding how global climate change will affect plants in real world soils. Field Crop Res 90: 101–115

Lynch J, Lauchli A, Epstein E (1991) Vegetative growth of the common bean in response to phosphorus nutrition. Crop Sci 31: 380–387

Ma QF, Longnecker N, Atkins C (2002) Varying phosphorus supply and development, growth and seed yield in narrow-leafed lupin. Plant Soil 239: 79–85

Ma Z, Bielenberg DG, Brown KM, Lynch JP (2001a) Regulation of root hair density by phosphorus availability in *Arabidopsis thaliana*. Plant Cell Environ 24: 459–467

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

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

Maina GG, Brown JS, Gersani M (2002) Intra-plant versus inter-plant root competition in beans: avoidance, resource matching or tragedy of the commons. Plant Ecol 160: 235–247

Mano Y, Omori F, Takamizo T, Kindiger B, Bird RM, Loaisiga CH (2006) Variation for root aerenchyma formation in flooded and non-flooded maize and teosinte seedlings. Plant Soil 281: 269–279

Mano Y, Omori F, Takamizo T, Kindiger B, Bird RM, Loaisiga CH, Takahashi H (2007) QTL mapping of root aerenchyma formation in seedlings of a maize x rare teosinte "*Zea nicaraguensis*" cross. Plant Soil 295: 103–113

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

Miguel M (2004) Genotypic variation in root hairs and phosphorus efficiency in common bean (*Phaseolus vulgaris* L.). Dissertation, Penn State University

Miller CR, Ochoa I, Nielsen KL, Beck D, Lynch JP (2003) Genetic variation for adventitious rooting in response to low phosphorus availability: potential utility for phosphorus acquisition from stratified soils. Funct Plant Biol 30: 973–985

Mollier A, Pellerin S (1999) Maize root system growth and development as influenced by phosphorus deficiency. J Exp Bot 50: 487–497

Neumann G, Martinoia E (2002) Cluster roots - an underground adaptation for survival in extreme environments. Trends Plant Sci 7: 162–167

Nielsen KL, Bouma TJ, Lynch JP, Eissenstat DM (1998) Effects of phosphorus availability and vesicular-arbuscular mycorrhizas on the carbon budget of common bean (*Phaseolus vulgaris*). New Phytol 139: 647–656

Nielsen KL, Eshel A, Lynch JP (2001) The effect of phosphorus availability on the carbon economy of contrasting common bean (*Phaseolus vulgaris* L.) genotypes. J Exp Bot 52: 329–339

Niklas K (1994) Plant Allometry: The Scaling of Form and Process. University of Chicago Press, Chicago, IL

Ochoa I, Blair M, Lynch J (2006) QTL analysis of adventitious root formation in common bean (*Phaseolus vulgaris* L.) under contrasting phosphorus availability. Crop Sci 46: 1609–1621

Oldeman L, Hakkeling R, Sombroek W (1991) World Map of the Status of Human-Induced Soil Degradation: An Explanatory Note (2nd revised edition). ISRIC, Wageningen, The Netherlands

Oldroyd GED, Harrison MJ, Udvardi M (2005) Peace talks and trade deals. Keys to long-term harmony in legume-microbe symbioses. Plant Physiol 137: 1205–1210

Ostertag R (2001) Effects of nitrogen and phosphorus availability on fine-root dynamics in Hawaiian montane forests. Ecology 82: 485–499

Owusu-Bennoah E, Zapata F, Fardeau JC (2002) Comparison of greenhouse and ^{32}P isotopic laboratory methods for evaluating the agronomic effectiveness of natural and modified rock phosphates in some acid soils of Ghana. Nutr Cycl Agroecosys 63: 1–12

Pellerin S, Mollier A, Plenet D (2000) Phosphorus deficiency affects the rate of emergence and number of maize adventitious nodal roots. Agron J 92: 690–697

Peng SB, Eissenstat DM, Graham JH, Williams K, Hodge NC (1993) Growth depression in mycorrhizal citrus at high-phosphorus supply - analysis of carbon costs. Plant Physiol 101: 1063–1071

Peterson RL, Farquhar ML (1996) Root hairs: specialized tubular cells extending root surfaces. Bot Rev 62: 1–40

Pothuluri J, Kissel D, Whitney D, Thien S (1986) Phosphorus uptake from soil layers having different soil test phosphorus levels. Agron J 78: 991–994

Radin J, Eidenbock M (1984) Hydraulic conductance as a factor limiting leaf expansion of phosphorus-deficient cotton plants. Plant Physiol 75: 372–377

Ray JD, Kindiger B, Dewald CL, Sinclair TR (1998) Preliminary survey of root aerenchyma in Tripsacum. Maydica 43: 49–53

Ray JD, Kindiger B, Sinclair TR (1999) Introgressing root aerenchyma into maize. Maydica 44: 113–117

Riedell WE, Reese RN (1999) Maize morphology and shoot CO_2 assimilation after root damage by western corn rootworm larvae. Crop Sci 39: 1332–1340

Robinson D (2005) Integrated root responses to variations in nutrient supply. In: BassiriRad H (ed), Nutrient Acquisition by Plants. An Ecological Perspective. Springer, Berlin/Heidelberg/New York, pp 43–62

Robinson D, Hodge A, Griffiths BS, Fitter AH (1999) Plant root proliferation in nitrogen-rich patches confers competitive advantage. Proc Roy Soc Lond B 266: 431–435

Roman-Aviles B, Snapp SS, Kelly JD (2004) Assessing root traits associated with root rot resistance in common bean. Field Crop Res 86: 147–156

Rossiter R (1978) Phosphorus deficiency and flowering time in subterranean clover *Trifolium subterraneum*. Ann Bot 42: 325–330

Rubio G, Walk T, Ge ZY, Yan XL, Liao H, Lynch JP (2001) Root gravitropism and below-ground competition among neighbouring plants: a modelling approach. Ann Bot 88: 929–940

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

Ryan MH, Graham JH (2002) Is there a role for arbuscular mycorrhizal fungi in production agriculture? Plant Soil 244: 263–271

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

Ryser P, Lambers H (1995) Root and leaf attributes accounting for the performance of fast-growing and slow-growing grasses at different nutrient supply. Plant Soil 170: 251–265

Setter TL, Waters I (2003) Review of prospects for germplasm improvement for waterlogging tolerance in wheat, barley and oats. Plant Soil 253: 1–34

Shane MW, Lambers H (2005) Cluster roots: a curiosity in context. Plant Soil 274: 101–125

Skene KR (2001) Cluster roots: model experimental tools for key biological problems. J Exp Bot 52: 479–485

Smith S, Read D (1997) Mycorrhizal Symbiosis. Academic, San Diego, CA

Smith SE, Smith FA, Jakobsen I (2003) Mycorrhizal fungi can dominate phosphate supply to plants irrespective of growth responses. Plant Physiol 133: 16–20

Snapp SS, Lynch JP (1996) Phosphorus distribution and remobilization in bean plants as influenced by phosphorus nutrition. Crop Sci 36: 929–935

Snapp S, Koide R, Lynch J (1995) Exploitation of localized phosphorus-patches by common bean roots. Plant Soil 177: 211–218

Snapp S, Kirk W, Roman-Aviles B, Kelly J (2003) Root traits play a role in integrated management of Fusarium root rot in snap beans. HortScience 38: 187–191

Soil Survey Staff (1999) Soil Taxonomy. A Basic System of Soil Classification for Making and Interpreting Soil Surveys (2nd edition). USDA/NRCS

Steen I (1998) Phosphorus availability in the 21st century. Management of a non-renewable resource. Phosphorus Potassium 217: 25–31

Steingrobe B, Schmid H, Claassen N (2001) Root production and root mortality of winter barley and its implication with regard to phosphate acquisition. Plant Soil 237: 239–248

Striker GG, Insausti P, Grimoldi AA, Leon RJC (2006) Root strength and trampling tolerance in the grass *Paspalum dilatatum* and the dicot *Lotus glaber* in flooded soil. Funct Ecol 20: 4–10

Striker GG, Insausti I P, Grimoldi AA, Vega AS (2007) Trade-off between root porosity and mechanical strength in species with different types of aerenchyma. Plant Cell Environ 30: 580–589

Tesfaye M, Temple SJ, Allan DL, Vance CP, Samac DA (2001) Overexpression of malate dehydrogenase in transgenic alfalfa enhances organic acid synthesis and confers tolerance to aluminum. Plant Physiol 127: 1836–1844

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

Ticconi CA, Abel S (2004) Short on phosphate: plant surveillance and countermeasures. Trends Plant Sci 9: 548–555

Tinker P, Nye P (2000) Solute Movement in the Rhizosphere. Oxford University Press, New York

Tomscha JL, Trull MC, Deikman J, Lynch JP, Guiltinan MJ (2004) Phosphatase under-producer mutants have altered phosphorus relations. Plant Physiol 135: 334–345

Van der Werf A, Welschen R, Lambers H (1992) Respiratory losses increase with decreasing inherent growth rate of a species and with decreasing nitrate supply: a search for explanations for these observations. In: Lambers H, Van der Plas L (eds), Molecular, Biochemical, and Physiological Aspects of Plant Respiration. SPB Academic Publishing, The Hague, pp 421–432

Vance CP (2008) Plants without arbuscular mycorrhizae. In: White PJ, Hammond JP (eds), The Ecophysiology of Plant-Phosphorus Interactions. Springer, Dordrecht, The Netherlands, pp 117–142

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

Vartapetian BB, Jackson MB (1997) Plant adaptations to anaerobic stress. Ann Bot 79: 3–20

Visser EJW, Colmer TD, Blom C, Voesenek L (2000) Changes in growth, porosity, and radial oxygen loss from adventitious roots of selected mono- and dicotyledonous wetland species with contrasting types of aerenchyma. Plant Cell Environ 23: 1237–1245

Walk T, Jaramillo R, Lynch J (2006) Architectural tradeoffs between adventitious and basal roots for phosphorus acquisition. Plant Soil 279: 347–366

Walker T (1965) The significance of phosphorus in pedogenesis. In: Hallsworth E, Crawford D (eds), Experimental Pedology. Butterworths, London, pp 295–316

Waters BM, Blevins DG (2000) Ethylene production, cluster root formation, and localization of iron (III) reducing capacity in Fe deficient squash roots. Plant Soil 225: 21–31

White PJ, Hammond JP (2008) Phosphorus nutrition of terrestrial plants. In: White PJ, Hammond JP (eds), The Ecophysiology of Plant-Phosphorus Interactions. Springer, Dordrecht, The Netherlands, pp 51–81

Whiteaker G, Gerloff G, Gabelman W, Lindgren D (1976) Intraspecific differences in growth of beans at stress levels of phosphorus. J Am Soc Hortic Sci 101: 472–475

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

Wood S, Sebastian K, Scherr S (2000) Pilot Analysis of Global Ecosystems: Agroecosystems. World Resources Institute, Washington, DC

World Bank (2004) World Development Indicators. Washington, DC

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

Wouterlood M, Lambers H, Veneklaas EJ (2005) Plant phosphorus status has a limited influence on the concentration of phosphorus-mobilising carboxylates in the rhizosphere of chickpea. Funct Plant Biol 32: 153–159

Xie YJ, Yu D (2003) The significance of lateral roots in phosphorus (P) acquisition of water hyacinth (*Eichhornia crassipes*). Aquat Bot 75: 311–321

Yan X (2005) The roots of P-efficient soybean: Theories and practices. In: Li CJ *et al.* (eds), Plant Nutrition for Food Security. Human Health and Environmental Protection, Tsinghia University Press, Beijing, China, pp 36–37

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

Yun SJ, Kaeppler SM (2001) Induction of maize acid phosphatase activities under phosphorus starvation. Plant Soil 237: 109–115

Zhao J, Fu J, Liao H, He Y, Nian H, Hu Y, Qiu L, Dong Y, Yan X (2004) Characterization of root architecture in an applied core collection for phosphorus efficiency of soybean germplasm. Chinese Science 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, Kaeppler SM, Lynch JP (2005a) Mapping of QTL for lateral root branching and length in maize (*Zea mays* L.) under differential phosphorus supply. Theor Appl Genet 111: 688–695

Zhu J, Kaeppler SM, Lynch JP (2005b) Topsoil foraging and phosphorus acquisition efficiency in maize (*Zea mays*). Funct Plant Biol 32: 749–762

Zhu J, Kaeppler SM, Lynch JP (2005c) Mapping of QTL controlling root hair length in maize (*Zea mays* L.) under phosphorus deficiency. Plant Soil 270: 299–310