TURNER REVIEW No. 14

Roots of the Second Green Revolution

Jonathan P. Lynch

Penn State, University Park, PA 16802, USA. Email: JPL4@psu.edu

Abstract. The Green Revolution boosted crop yields in developing nations by introducing dwarf genotypes of wheat and rice capable of responding to fertilisation without lodging. We now need a second Green Revolution, to improve the yield of crops grown in infertile soils by farmers with little access to fertiliser, who represent the majority of third-world farmers. Just as the Green Revolution was based on crops responsive to high soil fertility, the second Green Revolution will be based on crops tolerant of low soil fertility. Substantial genetic variation in the productivity of crops in infertile soil has been known for over a century. In recent years we have developed a better understanding of the traits responsible for this variation. Root architecture is critically important by determining soil exploration and therefore nutrient acquisition. Architectural traits under genetic control include basal-root gravitropism, adventitious-root formation and lateral branching. Architectural traits that enhance topsoil foraging are important for acquisition of phosphorus from infertile soils. Genetic variation in the length and density of root hairs is important for the acquisition of immobile nutrients such as phosphorus and potassium. Genetic variation in root cortical aerenchyma formation and secondary development ('root etiolation') are important in reducing the metabolic costs of root growth and soil exploration. Genetic variation in rhizosphere modification through the efflux of protons, organic acids and enzymes is important for the mobilisation of nutrients such as phosphorus and transition metals, and the avoidance of aluminum toxicity. Manipulation of ion transporters may be useful for improving the acquisition of nitrate and for enhancing salt tolerance. With the noteworthy exceptions of rhizosphere modification and ion transporters, most of these traits are under complex genetic control. Genetic variation in these traits is associated with substantial yield gains in low-fertility soils, as illustrated by the case of phosphorus efficiency in bean and soybean. In breeding crops for low-fertility soils, selection for specific root traits through direct phenotypic evaluation or molecular markers is likely to be more productive than conventional field screening. Crop genotypes with greater yield in infertile soils will substantially improve the productivity and sustainability of low-input agroecosystems, and in high-input agroecosystems will reduce the environmental impacts of intensive fertilisation. Although the development of crops with reduced fertiliser requirements has been successful in the few cases it has been attempted, the global scientific effort devoted to this enterprise is small, especially considering the magnitude of the humanitarian, environmental and economic benefits being forgone. Population growth, ongoing soil degradation and increasing costs of chemical fertiliser will make the second Green Revolution a priority for plant biology in the 21st century.

The need for a second Green Revolution

By the middle of the 20th century, prospects for food security in developing nations were grim. Food production was not keeping pace with burgeoning populations and cereals had limited responsiveness to fertiliser inputs because they would lodge at high fertility (Curve 1 in Fig. 1). In response to this challenge, Norman Borlaug and others developed dwarf genotypes of rice and wheat that were capable of responding to fertilisers without lodging (Curve 2 in Fig. 1). The resulting 'Green Revolution' substantially increased grain production and averted disaster, making it one of the most important agricultural innovations of the 20th century (Borlaug 1972; Khush 1999). My goal here is to consider prospects for a second Green Revolution, which would boost yields at lower fertility (Curve 3 in Fig. 1).

We need a second Green Revolution. The technology package of fertilisers and improved cereal varieties that comprised the first Green Revolution was not available to many of the neediest people, because of poverty, lack of access to inputs, credit and markets, and because many third-world agroecosystems rely on crops other than wheat and rice (Shiva 1991). We now confront a silent food crisis, one that seldom intrudes into the public consciousness in the wealthy nations, but that is nonetheless a humanitarian disaster of epic proportions. According to recent estimates, 854 million people are malnourished, 6 million children under the age of 5 die each year from hunger, and more than half of all childhood deaths in the developing world are caused directly or indirectly by malnutrition (FAO 2002). The Food and Agriculture Organisation (FAO) of the United Nations recently stated that 'FAO's latest estimates of the number of undernourished people confirm an alarming trend—progress in reducing hunger in the developing world has slowed to a crawl and in most regions the number of undernourished people is actually growing' (FAO 2002).

World hunger is a multifaceted problem, associated with diverse interrelated causes including overpopulation, poverty, disease, environmental degradation, war, social inequity,
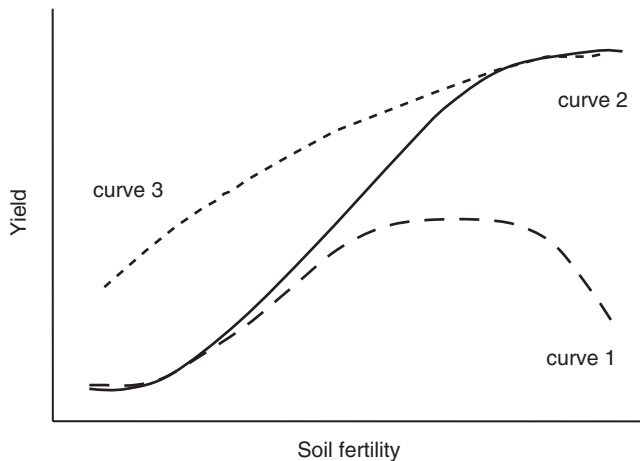
Fig. 1. Crop yield response to nutrient availability. Curve 1 shows the response of wheat and rice to nitrogen availability before the Green Revolution; yields declined at high N fertility because of lodging. Curve 2 shows the enhanced yield in high-fertility soil of dwarf (non-lodging) genotypes of wheat and rice that comprised the Green Revolution. Curve 3 shows enhanced crop yield across fertility levels that is the goal of the second Green Revolution.

ignorance, corruption, lack of infrastructure and so on. Although this makes the problem seem intractable, it also represents an opportunity, since improvements in food security can be introduced from many directions. The most direct contribution to food security would simply be improved food production in developing nations. Improved food production directly improves the food security of subsistence farmers, reduces the cost of food for poor consumers and enhances rural incomes (Vosti and Reardon 1997; Runge *et al.* 2003). These benefits are especially relevant in developing countries, which typically have a large proportion of the labour force in agriculture (World Bank 2004). Improved food production would have substantial benefits for food security in the developing world.

There is substantial opportunity to improve crop yields in developing countries, since current yields are often a small fraction of yield potential (Table 1). Low soil fertility and drought are primary causes of low yields in developing countries. Global geographic analyses have demonstrated that edaphic constraints such as low phosphorus availability and soil acidity characterise vast areas of the developing world (Fig. 2). The primary importance of edaphic factors as yield limitations is confirmed by more detailed analysis of agroecological constraints for specific crops, such as common bean, in which well over half of production zones in Africa and Latin America have serious soil-fertility problems (Table 2). Such analyses show that drought, low phosphorus availability, low nitrogen availability, and soil acidity, which usually includes aluminum toxicity, low availability of calcium, magnesium, and potassium, and often includes manganese toxicity, are the most pervasive edaphic constraints in third-world agriculture (Sanchez 1976, 2002). These analyses are often based on native soil fertility, which often substantially overestimates the actual soil fertility because of soil degradation and nutrient depletion. Approximately 40% of the agricultural land in the world has been significantly degraded by human activity, including more than 75% of the agricultural soils of Africa (UNEP; http://maps. grida.no/go/graphic/global_soil_degradation). Decades of low-input agriculture have also resulted in substantial depletion of soil nutrient reserves (Newman 1997; Hartemink 2003; Sanchez and Swaminathan 2005). Fertilisers are not a satisfactory solution to this problem, because of their cost (which has risen substantially in recent years owing to increased fuel prices), limited availability (Steen 1998), the fact that many tropical soils have poor responsiveness to fertilisers, and soil degradation from inappropriate fertiliser use. In fact, fertiliser use is negligible in many developing countries, especially in sub-Saharan Africa, which generally have the poorest soils (Fig. 3). What is needed is *integrated nutrient management*, consisting of judicious use of fertility inputs as available, management practices to conserve and enhance soil fertility,

Table 1.   Yield of staple crops

| | Average yield 2003–2005 (metric t ha^{-1})[A] | | | | | |
	Maize	Bean	Rice (paddy)	Wheat	Sorghum	Millet
Africa, developing	1.4	0.6	2.0	2.2	0.85	0.68
Africa, developed	3.1	1.4	2.3	2.2	3.3	0.57
Asia, developing	4.0	0.6	4.0	2.9	1.0	1.0
Asia, developed	15.9	2.0	6.3	3.6	2.9	1.0
Latin America and Carribean	3.3	0.8	3.9	2.6	3.0	1.7
Latin America, developed	10.8	1.9	4.8	4.4	–	–
Developed countries (world)	7.8	1.7	6.5	2.9	3.7	1.3
United States	9.4	1.8	7.5	2.9	4.0	1.3
Yield potential with high water and nutrient input	20[B]	5.8[C]	10[D]	10[E]	4.0[F]	4.3[G]

[A]FAOSTAT [last update 24 January 2006]. Africa, developed: South Africa; Asia, developed: Japan, Israel; Latin America, developed: Chile; World, developed: Albania, Armenia, Australia, Austria, Republic of Azerbaijan, Belarus, Belgium, Belgium–Luxembourg, Bosnia and Herzegovina, Bulgaria, Canada, Croatia, Czech Republic, France, Georgia, Germany, Greece, Hungary, Israel, Italy, Japan, Kazakhstan, Kyrgyzstan, Luxembourg, the former Yugoslav Republic of Macedonia, Republic of Moldova, The Netherlands, New Zealand, Poland, Portugal, Romania, Russian Federation, Serbia and Montenegro, Slovakia, Slovenia, South Africa, Spain, Switzerland, Tajikistan, Turkmenistan, Ukraine, United Kingdom, United States of America, Uzbekistan.
[B]Tollenaar and Lee (2002); [C]Beaver *et al.* (2003); [D]Peng *et al.* (1999); [E]Tripathi *et al.* (2004);
[F]Baumhardt *et al.* (2005); [G]van Oosterom *et al.* (2003).

(a) Average soil suborder pH

pH values

- Rock
- Ice
- Water
- pH <= 4.5
- 4.5 < pH <= 5
- 5 < pH <= 5.5
- 5.5 < pH <= 6
- pH > 6

(b) Average soil suborder phosphorus availability

Average P values (ppm)

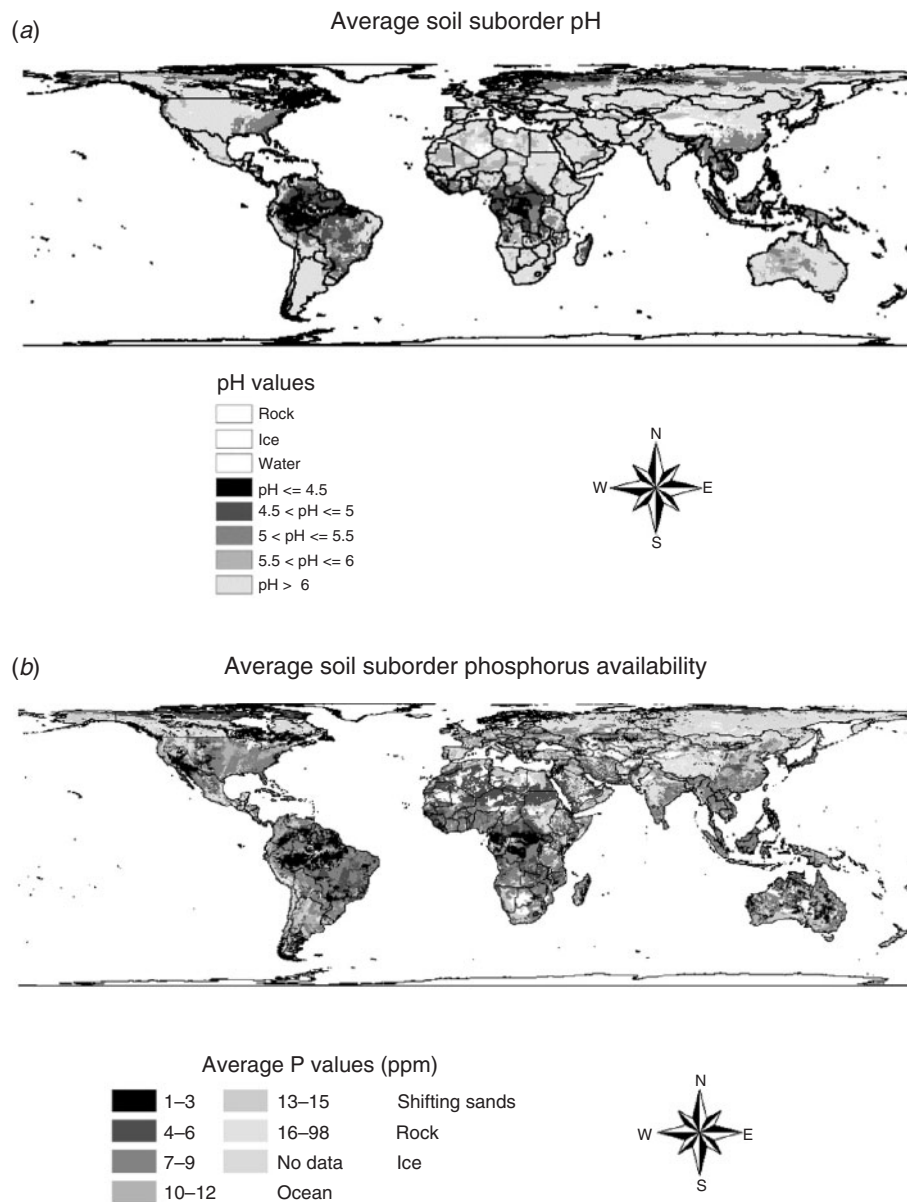|		
1–3	13–15	Shifting sands
4–6	16–98	Rock
7–9	No data	Ice
10–12	Ocean	

Fig. 2. Global distribution of soil suborders (USDA Soil Taxonomy 1999) (*a*) with acidity and (*b*) low phosphorus availability. (*a*) Soil acidity less than pH 5.5 is associated with decreasing availability of phosphorus, calcium, magnesium, and potassium, and increasing risk of manganese toxicity, and less than pH 5 with increasing risk of aluminium toxicity. (*b*) Global soil phosphorus availability; most annual crops require 15 ppm.

and adapted germplasm capable of superior growth and yield in low-fertility soil.

Although genetic variation for crop growth in low-fertility soil has been known for at least 120 years (Anonymous 1887), the potential for this technology is not widely recognised. In this paper, I will summarise in broad terms the feasibility of developing crops with superior growth in low-fertility soil, focusing on promising traits and outstanding issues, with examples drawn mainly from phosphorus acquisition efficiency, defined as the relative ability of a crop to grow and yield at suboptimal phosphorus availability (Lynch 1998). Improved (macro)nutrient acquisition efficiency (NAE) is in general a

more promising breeding goal than improved (macro)nutrient utilisation efficiency (NUE), for several reasons, including the following: (1) shoot traits affecting NUE such as phenology are often confounded with other traits of interest to breeders, (2) NUE has already been subject to indirect selection in decades of breeding for yield potential, (3) in contrast, root traits related to NAE may have been subject to neutral or negative selection by modern breeding under high-input conditions and (4) root traits related to NAE have very rarely been used as selection criteria, and represent an untapped pool of useful phenotypic variation. The scope of topics addressed here precludes a comprehensive review of relevant literature. Where possible I

Table 2. Extent of edaphic stress in common bean (*Phaseolus vulgaris*) production in developing regions

Values are the percentage of bean production area severely affected by the indicated stress, based on GIS analysis; –, indicates no data

Edaphic stress	South America	Central America	East Africa	South Africa
Low P	55	62	65	85
Al toxicity	40	19	55	44
Mn toxicity	12	25	50	35
Low Ca	36	19	–	–
Low K	15	10	55	50
Low Mg	23	23	–	–

have attempted to cite recent reviews for more detailed overviews of specific topics.

Root traits of the second Green Revolution

Root growth

A common response to suboptimal nutrient availability is an increase in the relative allocation of biomass to roots, typically 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 is allometric, i.e. root : shoot ratios normally decline with growth, and since plants in infertile soils grow more slowly, their root : shoot ratios are greater at a given plant age. However, when this factor is eliminated by comparison of allometric partitioning coefficients among plants grown at different phosphorus levels, phosphorus-efficient genotypes maintained a greater root : shoot ratio (greater allometric partitioning coefficient to roots), made possible by reduced respiratory costs of root growth (Nielsen *et al.* 2001). Low phosphorus and nitrogen availabilities reduce leaf appearance, leaf expansion and shoot branching (Radin and Eidenbock 1984; Lynch *et al.* 1991). Among annuals, phosphorus stress decreased shoot growth in dicots more than in monocots, possibly because of differences in leaf morphology (Halsted and Lynch 1996).

Although root growth has obvious importance for acquisition of soil resources, it is particularly important for the acquisition of immobile resources. Nutrients that are soluble in water are brought to the root primarily via transpiration-driven mass flow, whereas diffusion-limited nutrients, including phosphorus and potassium, must be acquired by roots (or root symbionts) in close proximity (Table 3, Barber 1995). It is therefore not surprising that root growth is regulated by phosphorus availability. Low phosphorus availability changes the distribution of growth among various root types. In bean, growth of primary- and basal-root axes is maintained under low phosphorus, whereas initiation of lateral roots is reduced, so that lateral-root density declines (Borch *et al.* 1999). In phosphorus-starved maize, axile (seminal and nodal)-root elongation and lateral-root density were unaffected, but lateral-root elongation was first promoted slightly, then severely retarded, as phosphorus starvation proceeded (Mollier and Pellerin 1999). Sustained elongation of axile roots in maize and bean could be interpreted as exploratory behaviour, allowing these roots to encounter localised patches of higher phosphorus availability. When the main root of a phosphorus-deficient plant encounters a patch of higher nutrient availability, lateral roots may proliferate within the patch (Robinson 2005). The response of the length and number of lateral roots to phosphorus stress varies substantially among maize genotypes, with some genotypes increasing and others decreasing lateral rooting (Zhu and Lynch 2004). Genotypes with increased or sustained lateral-root development under phosphorus deficiency had superior ability to acquire phosphorus and maintain growth. In bean, some genotypes respond to low phosphorus availability by preferentially increasing the production of adventitious roots, which have the advantages of low construction cost and location in the nutrient-rich topsoil (Miller *et al.* 2003).
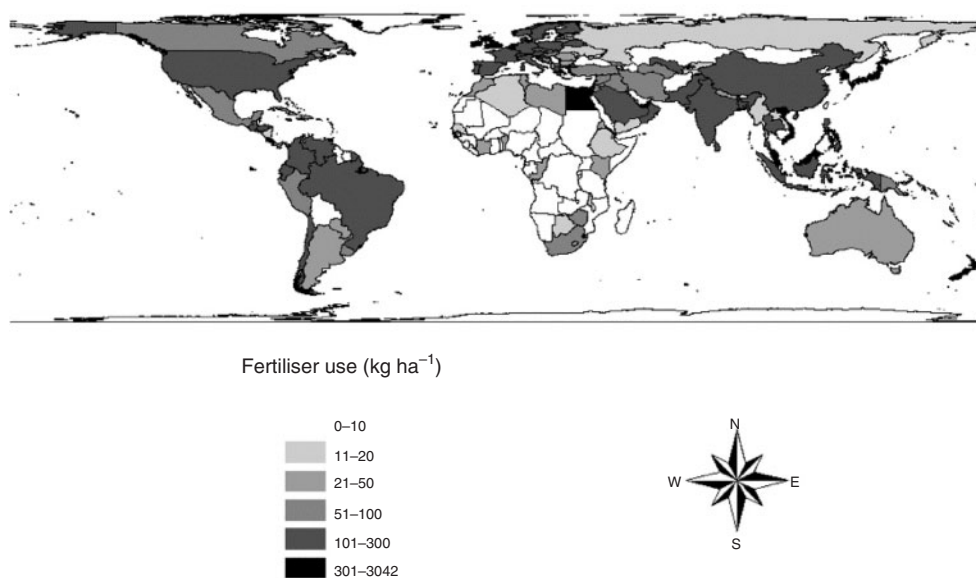

Fertiliser use (kg ha^{-1})

- 0–10
- 11–20
- 21–50
- 51–100
- 101–300
- 301–3042

N W E S

Fig. 3. Global distribution of fertiliser use (as national averages) in 1999–2001, in kilograms fertiliser per hectare of arable land.

Table 3. Significance of root interception, mass flow and diffusion in supplying maize with nutrients (kg ha^{-1})

Nutrient	Amount needed for 9.5 Mg yield of dry grain ha^{-1}	Approximate amounts supplied by		
		Root interception	Mass flow	Diffusion
Nitrogen	190	2	150	38
Phosphorus	40	1	2	37
Potassium	195	4	35	156
Calcium	40	60	150	0
Magnesium	45	15	100	0
Sulfur	22	1	65	0

In the context of crop breeding, selection of genotypes with abundant root production may be counterproductive, as the metabolic costs of root growth and maintenance can be a significant drain on reproductive output, especially in low-fertility environments. Several studies have shown that the metabolic costs of soil exploration by root systems are quite substantial, and can exceed 50% of daily photosynthesis (Nielsen *et al.* 1998, 2001; Lambers *et al.* 2002). Following the economic paradigm of plant resource allocation (Bloom *et al.* 1985), 'cost' denotes metabolic investment, including the production and maintenance of tissues, often measurable in units of carbon (Lynch and Ho 2005). All else being equal, a plant that is able to acquire a limiting soil resource at a reduced metabolic cost will have superior productivity, because it will have more metabolic resources available for further resource acquisition, growth and reproduction. Traits that enhance the effectiveness or efficiency of roots in acquiring soil resources would be better selection targets than root size *per se*.

Root architecture

Root architecture, the spatial configuration of the root system over time, is critically important for soil resource acquisition, by determining the deployment of root foraging in distinct soil domains, and the extent of competition for soil resources among roots of the same or neighbouring plants (Lynch 2005).

Because the topsoil is generally the soil stratum with the greatest phosphorus bioavailability, the extent of topsoil foraging is an important aspect of phosphorus acquisition in most soils (Lynch and Brown 2001). Genetic differences in adaptation to low soil phosphorus availability among genotypes of maize and bean are associated with the extent of topsoil foraging (Bonser *et al.* 1996; Ge *et al.* 2000; Liao *et al.* 2001; Ho *et al.* 2005; Zhu *et al.* 2005c). Architectural traits associated with enhanced topsoil foraging include shallower growth of basal roots, enhanced adventitious rooting and greater dispersion of lateral roots (Fig. 4). There are several lines of evidence that shallower basal-root growth enhances topsoil foraging and thereby phosphorus acquisition. Geometric modelling was used to evaluate the effect of changing basal-root gravitropism on phosphorus acquisition (Ge *et al.* 2000). This study showed that in soils with uniform phosphorus distribution, shallower root systems explored more soil per unit of root biomass than did deeper systems, because shallower systems have more dispersed basal roots and therefore less competition with neighbouring roots. In simulations with more phosphorus enrichment of the topsoil, shallower root systems acquired more phosphorus than did deep ones, by concentrating root foraging in the soil domain with greatest phosphorus availability. These simulation results are supported by several empirical studies with bean showing good correlation of basal-root growth angle with
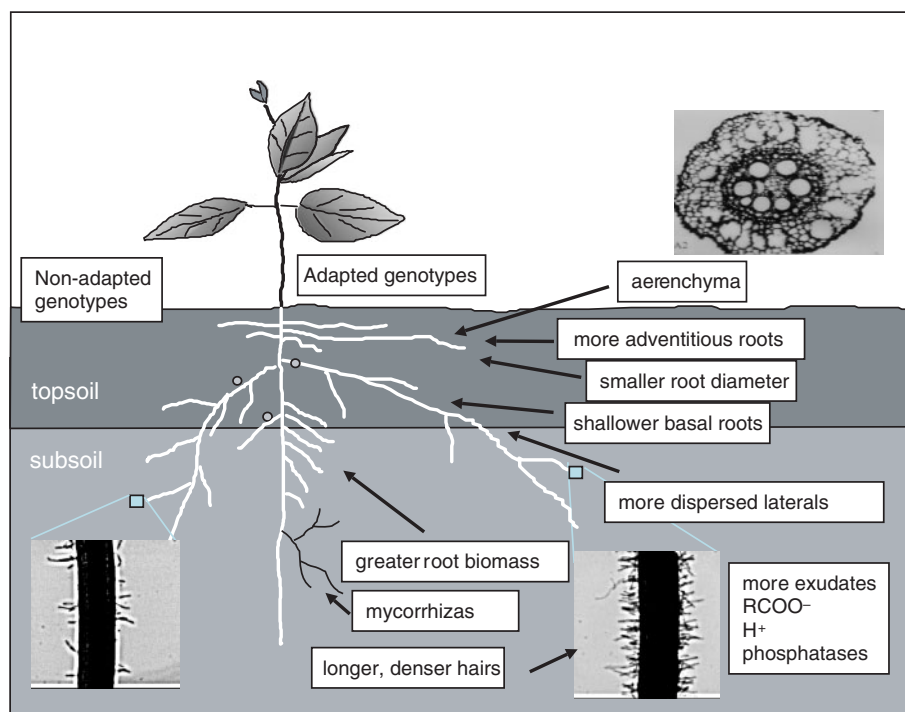

Fig. 4. Root adaptations to low phosphorus availability, as discussed in the text.

phosphorus uptake from low-phosphorus soil (Fig. 5a; Liao *et al.* 2001), with yield in field trials in low-phosphorus tropical soils (Fig. 5b; Bonser *et al.* 1996) and with growth in a low-phosphorus field trial in Honduras (Ho *et al.* 2005). Genetic mapping in bean revealed co-segregation of quantitative trait loci (QTL) for root shallowness and phosphorus 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-phosphorus soils in the field and greenhouse (Zhu *et al.* 2005c). Similar results have been observed with soybean (X. Yan, pers. comm.). It therefore appears that shallowness of basal roots is an important trait for topsoil foraging and efficiency of phosphorus acquisition in annual crops.

Adventitious rooting from subterranean hypocotyl (in dicots) or mesocotyl (in monocots) tissue is another element of topsoil exploration by the root system. Bean genotypes differ substantially in their extent of adventitious rooting and in the regulation of adventitious rooting by phosphorus (Miller *et al.* 2003; Ochoa *et al.* 2006). A field study in a low-phosphorus tropical soil showed that bean genotypes with greater growth and phosphorus uptake had more adventitious rooting re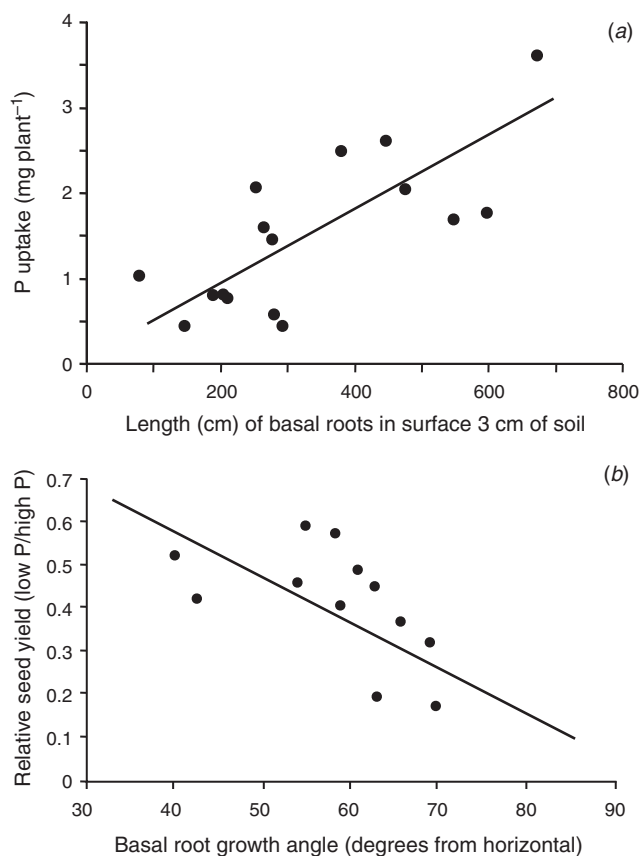lative to basal root growth than did phosphorus-inefficient genotypes (Miller *et al.* 2003). Adventitious roots may have several benefits for topsoil exploration. Obviously, their horizontal growth concentrates their foraging activity in the topsoil. Other advantages may relate to the anatomical and morphological differences between adventitious roots and basal roots. In bean, adventitious roots have greater specific root length (SRL, root length per unit root mass) than do other root types (Fig. 6). 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 Ho 2005). 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 across larger soil volumes for a given metabolic investment (Miller *et al.* 2003). Genetic mapping of adventitious rooting in bean identified several major QTL, including a pair of QTL that accounted for an impressive 61% of observed phenotypic variation for adventitious rooting in the field under low-phosphorus conditions, supporting the feasibility of selection for this trait in crop breeding (Ochoa *et al.* 2006).

A third component of root architecture that is important for phosphorus acquisition is lateral rooting. Substantial genetic variation for lateral rooting exists in maize (Zhu and Lynch 2004; Zhu *et al.* 2005a). Genotypes with enhanced or sustained lateral rooting at low phosphorus availability had greater phosphorus acquisition and biomass accumulation and a higher relative growth rate than did genotypes with reduced lateral rooting (Zhu and Lynch 2004). Genotypes varied in the phosphorus investment required for lateral-root elongation, owing to genetic differences in the SRL and phosphorus concentration of the lateral roots. Lateral-root extension required less biomass and phosphorus investment than the extension of other root types. Two distinct cost–benefit analyses—one with phosphorus
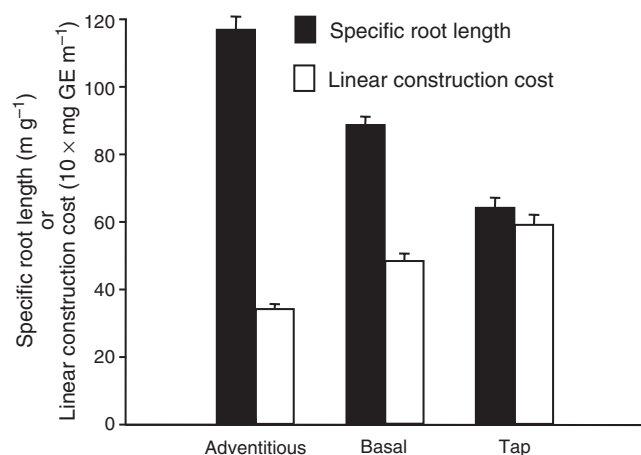

Fig. 5. (a) Correlation of basal-root shallowness with phosphorus uptake from low-phosphorus soil ($r = 0.74$, $P < 0.01$) and (b) correlation of basal root growth angle 5 days after germination with yield in a field study in low-phosphorus soil ($r = 0.32$, $P = 0.067$) in common bean. Data from (a) Liao *et al.* (2001) and (b) Bonser *et al.* (1996).

Fig. 6. Variation among root classes of common bean in metabolic cost of soil exploration, measured by specific root length in meters of root length per gram of root dry weight, and linear construction cost in milligrams of glucose equivalents per metre of root length. Each bar is the mean of four replicates, ± s.e. Differences among root classes within a variable are highly significant ($P < 0.001$). Data are extracted from Miller *et al.* (2003).

acquisition rate as a benefit and root respiration as a cost, the other with plant phosphorus accumulation as a benefit and phosphorus allocation to lateral roots as a cost—showed that lateral rooting was advantageous under conditions of low phosphorus availability (Zhu and Lynch 2004). Genetic mapping of lateral rooting in maize identified QTL for the length, number and plasticity of lateral roots with contrasting phosphorus supply (Zhu *et al.* 2005*b*). The detection of QTLs for these traits, in combination with the observation of substantial transgressive segregation, indicates that favourable alleles can be combined to increase seedling lateral-root growth in maize. These results suggest that enhanced lateral rooting under phosphorus stress may be harnessed as a useful trait for the selection and breeding of more phosphorus-efficient maize genotypes.

Although there is good evidence for the importance of root architectural traits for phosphorus acquisition, less is known regarding the importance of specific architectural traits for the acquisition of mobile nutrients such as nitrate, calcium and magnesium. The greater mobility of these nutrients would make their acquisition less dependent on root proximity and, therefore, the fine structure of root architecture. This is supported by the observation that in *Arabidopsis*, a mutation affecting lateral roots had a greater impact on phosphorus acquisition than on nitrogen acquisition (Fitter *et al.* 2002). The coarse structure of root architecture, especially the lateral spread and depth of root foraging, may be important for the acquisition of soluble nutrients, especially nitrate. Geometric modelling indicates that an efficient root architecture for nitrate capture in well drained Mediterranean environments would include vigorous topsoil foraging early in the season to capture nitrate leached with opening season rains, coupled with vigorous taproot growth to exploit nitrate leached later in the season (Dunbabin *et al.* 2003). The co-optimisation of root architecture for the acquisition of multiple soil resources, considering interplant competition and the stochastic distribution of resources in time and space (Ho 2004), is a challenging problem in root biology. The importance of these traits for soil adaptation, as well as the large genetic variation for root architecture, make them priority targets of selection programs.

Root anatomy and morphology

Root hairs are subcellular protrusions of root epidermal cells that are important for the acquisition of immobile nutrients such as phosphorus by expanding the volume of soil subject to phosphorus depletion through diffusion to the root surface (Fig. 7, Clarkson 1985; Peterson and Farquhar 1996; Jungk 2001). The importance of root hairs for phosphorus acquisition has been demonstrated by simulation modelling (Bouldin 1961; Itoh and Barber 1983*a*, 1983*b*), autoradiography (Lewis and Quirk 1967; Bhat and Nye 1974), analysis of root-hair mutants (Bates and Lynch 2000*a*, 2000*b*, 2001; Gahoonia and Nielsen 2003) and comparison of contrasting species (Itoh and Barber 1983*b*; Foehse *et al.* 1991; Gahoonia *et al.* 1999) and genotypes of the same species (Caradus 1981; Gahoonia and Nielsen 1997; Gahoonia *et al.* 1997, 2001; Miguel 2004; Yan *et al.* 2004). Root hairs manifest several distinct phenotypic traits that are co-regulated by phosphorus availability, including root-hair length, density (i.e. number of root hairs per unit root-

surface area), distance of appearance from the root tip and the pattern of root trichoblasts or hair-bearing cells (Bates and Lynch 1996; Ma *et al.* 2001*a*, 2001*b*). Geometric modelling indicated that these distinct traits interact synergistically to improve phosphorus acquisition; the combined effect of all four root-hair traits on phosphorus acquisition was 371% greater than their additive effects (Ma *et al.* 2001*b*). In addition to their importance in extending the effective depletion zone for phosphorus uptake, root hairs may also assist the dispersion of exudates such as carboxylates throughout the rhizosphere, which improves phosphorus bioavailability in many soils (Hinsinger 2001; Ryan *et al.* 2001). Direct metabolic costs associated with root hairs are slight (Bates and Lynch 2000*b*). Genotypic variation in root-hair length and density in maize and bean is controlled by several major QTL (Yan *et al.* 2004; Zhu *et al.* 2005*a*), suggesting that this trait could be selected in breeding programs through marker-aided selection as well as through direct phenotypic screening. Genotypic variation in root-hair length and density is important for phosphorus acquisition regardless of the mycorrhizal status of the plant (Fig. 8, Miguel 2004). The large genotypic variation for root-hair traits, and the substantial effect this variation has on phosphorus acquisition, regardless of mycorrhizal status, together with the relatively simple genetic control of these traits and opportunities for direct phenotypic selection, make them attractive targets for crop breeding (Gahoonia and Nielsen 2004).

Aerenchyma denotes tissue with large intercellular spaces (Fig. 9, Esau 1977). Although root cortical aerenchyma is a well known adaptation to hypoxia (reviewed in Jackson and Armstrong 1999), it is less commonly recognised that root aerenchyma can also be induced by suboptimal availability of nitrogen, phosphorus and sulfur (Konings and Verschuren 1980; Drew *et al.* 1989; Eshel *et al.* 1995; Lu *et al.* 1999; Bouranis *et al.* 2003; Fan *et al.* 2003). It has been proposed that aerenchyma formation is adaptive for nutrient-stressed roots, since the replacement of living cortical cells by air space would reduce the carbon and nutrient requirements of the root tissue (Lynch and Brown 1998; Fan *et al.* 2003). Genotypic variation in aerenchyma formation in maize is associated with reduced respiration of root segments and whole root systems (Fig. 10, Fan *et al.* 2003) and with enhanced root growth in low-phosphorus soil in the field (Fig. 11). The large genotypic variation (200–300%) in aerenchyma formation in response to phosphorus stress in both maize and common bean (Fig. 9, Fan *et al.* 2003) raises interesting questions regarding the adaptive importance and functional tradeoffs for aerenchyma in diverse environments. Tradeoffs to aerenchyma formation may include reduced root habitat for mycorrhizal fungi, reduced radial transport of water and nutrients, reduced root vacuolar storage capacity and increased axial spread of pathogenic fungi. The large intraspecific variation in important crop species makes aerenchyma amenable to plant breeding, currently underway to enhance flooding tolerance (Ray *et al.* 1999; Setter and Waters 2003).

Another means to reduce the metabolic cost of soil exploration is by 'root etiolation', i.e. reducing root diameter or tissue density under nutrient stress so that each gram of root tissue can explore a greater soil volume (Fig. 12, Lynch and Brown 2006). Reduction of root diameter can be caused
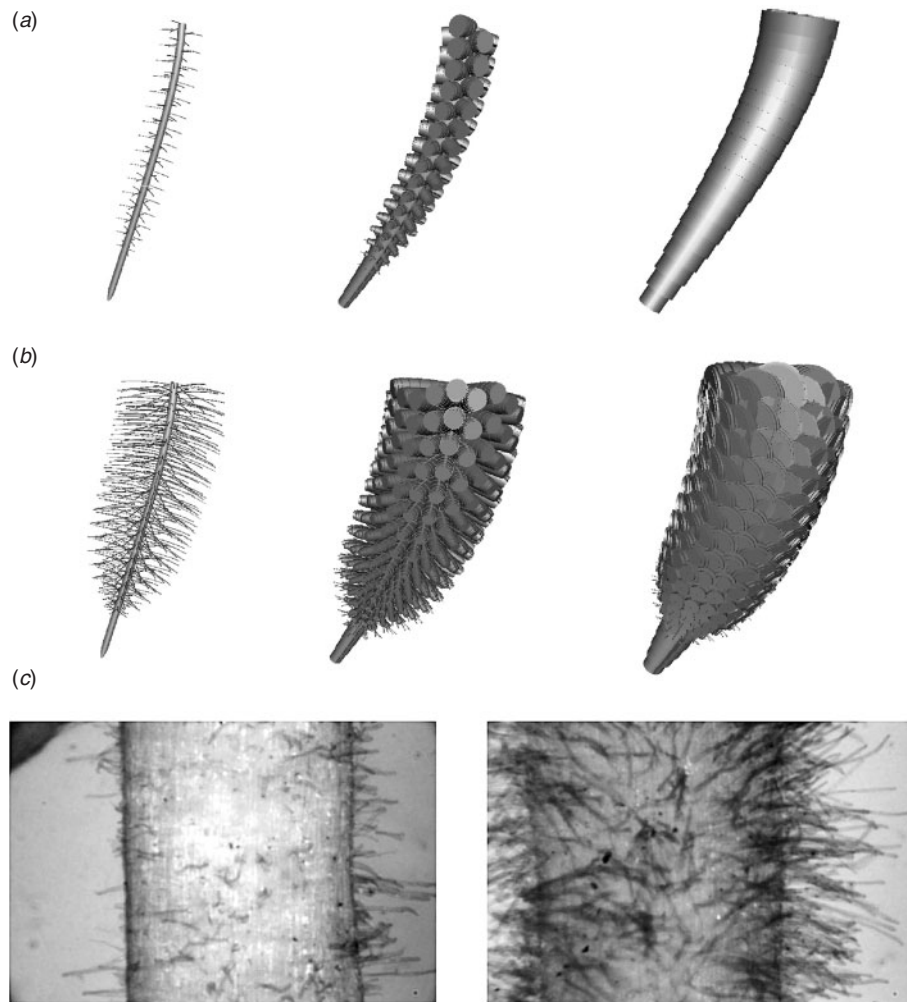
Fig. 7. Root hairs. Geometric simulation model of (*a*) the short, sparse root hairs of *Arabidopsis thaliana* grown with high phosphorus availability and (*b*) long, dense root hairs of *A. thaliana* grown under low phosphorus availability, showing the root itself (left image) and zones of phosphorus depletion at low (centre image) and high (right image) soil phosphorus mobility. (*c*) Genetic variation in the length and density of root hairs found in cultivars of common bean. (*a*) and (*b*) are based on Ma *et al*. (2001*a*).

by low availability of nitrate (Hackett 1972; Drew and Saker 1978; Ryser and Lambers 1995) and phosphorus (Xie and Yu 2003; Zhu and Lynch 2004). Under low phosphorus availability, root elongation is maintained at the expense of lateral branching (Borch *et al*. 1999) and secondary growth (Eshel *et al*. 1995). Large genotypic variation exists for the diameter of axial and lateral roots in maize, with smaller root diameter being associated with greater SRL of lateral roots, faster lateral-root growth, greater shoot growth and phosphorus efficiency (Zhu and Lynch 2004). Potential tradeoffs to this trait include reduced ability to penetrate hard soil and greater susceptibility to root herbivores and pathogens.

Root exudates

Aluminum toxicity is a principal constraint to crop production in acid soils (pH < 5.2, Fig. 2). Soluble aluminum stunts root elongation and reduces the uptake of phosphorus, calcium, magnesium and potassium, which are already poorly available

in most acid soils. Substantial genetic variation in aluminum tolerance has been demonstrated for many years, including classic studies by Foy and others in the 1960s showing large genetic variation among crop species for aluminum tolerance (Foy *et al*. 1978). Considerable research on the mechanism of aluminum tolerance in crops has identified the production of root exudates, specifically, carboxylates such as malate and citrate, in the tolerance mechanism (Kochian *et al*. 2005), although alternative aluminum tolerance mechanisms exist (e.g. Piñeros *et al*. 2005). These organic anions can chelate trivalent aluminum ions, thereby protecting the root tips from aluminum toxicity. The genetic control of carboxylate exudation is relatively simple, and in several species is governed by one or two genes, enhancing the prospect of transgenic approaches or direct genotype selection for improving the aluminum tolerance of crops (Kochian *et al*. 2005). Overexpression of enzymes responsible for organic acid production in roots improves plant growth in soils with excess aluminum or deficient phosphorus
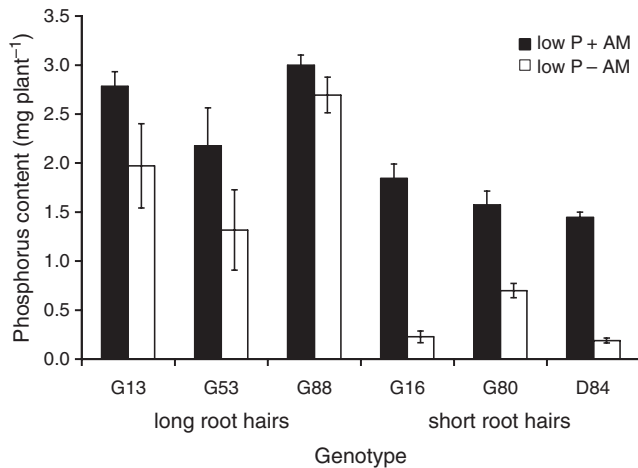
Fig. 8. Effects of root-hair length and mycorrhizal inoculation on phosphorus content (mean ± s.e.m., $n = 4$) of common bean genotypes. Plants were grown for 28 days in low-phosphorus soil with (+AM) or without (−AM) arbuscular mycorrhizal inoculum. Genotypes are recombinant inbred lines, with either long or short root hairs. ANOVA indicated that genotypes with long root hairs had greater phosphorus content than genotypes with short root hairs either with or without AM inoculation ($n = 4$). Data are from Miguel (2004).

(Koyama *et al.* 2000; Lopez-Bucio *et al.* 2000*a*; Tesfaye *et al.* 2001). By allowing roots to continue growing in acid soils, aluminum tolerance has substantial benefits for nutrient (and water) acquisition, and therefore is a critical component of the second Green Revolution.

Carboxylate exudation is also important for phosphorus solubilisation in the rhizosphere, especially from phosphorus-fixing soils (Fig. 13). Carboxylates chelate Al^{3+}, Fe^{3+} and Ca^{2+}, which results in mobilisation of phosphate from bound forms, and promote anion exchange of phosphate from iron and aluminum oxide surfaces (Ryan *et al.* 2001). This activity is complemented in neutral and alkaline soils by rhizosphere acidification, which results in increased solubility of calcium phosphates (Hinsinger 2001). The importance of carboxylate exudation for phosphorus mobilisation in the rhizosphere has been discussed extensively in several recent reviews (Lopez-Bucio *et al.* 2000*b*; Hinsinger 2001; Ryan *et al.* 2001).

Root exudates are also important for the acquisition of micronutrient metals such as iron and zinc, which are poorly available in alkaline soils. Substantial genetic variation exists for iron and zinc uptake from such soils (Ali *et al.* 2002), associated with metal mobilisation in the rhizosphere via protons, phenolics and organic acids in dicots and with phytosiderophores in cereals (Neumann and Römheld 2002; Rengel 1999, 2002). Exploitation of this variation is part of a major international effort to breed staple foods with greater micronutrient density ('HarvestPlus': www.harvestplus.org) to address global micronutrient deficiencies in the human diet (Welch and Graham 2004).

Since a considerable proportion of soil phosphorus may occur in organic forms, plants may increase phosphorus availability in the rhizosphere by secreting phosphohydrolases to mineralise phosphate from organic compounds (Marschner 1995; Abel *et al.* 2002; Vance *et al.* 2003). Secreted acid phosphatases can be up-regulated under phosphorus deficiency (Goldstein 1992; Tomscha *et al.* 2004). Recent work has demonstrated their significance for phosphorus nutrition under phosphorus-limiting conditions (Li *et al.* 2003, 2004; Tomscha *et al.* 2004), although their importance seems to vary with species, cropping system and forms of organic phosphorus in the soil (Yun and Kaeppler 2001; Li *et al.* 2003, 2004; George *et al.* 2005).

Root exudates receive considerable research attention. They are clearly important for aluminum tolerance and phosphorus uptake from low-fertility soils, and unlike many other root traits, are under relatively simple genetic control. Indeed, in the case of phosphatases the trait is itself a gene product. The genetic simplicity of these traits is counteracted to some degree by the bewildering complexity of the fate of these compounds in the rhizosphere, especially considering the microbial population of the rhizosphere, and the large variation in exudate production in different soils (Jones *et al.* 2003; Veneklaas *et al.* 2003; Hinsinger *et al.* 2005). Increasing availability of sequence information for major genes controlling root exudates make these traits attractive targets for genetic manipulation.

Ion transporters

The transport of ions and water across biological membranes is mediated by proteins (Chrispeels *et al.* 1999). The relative
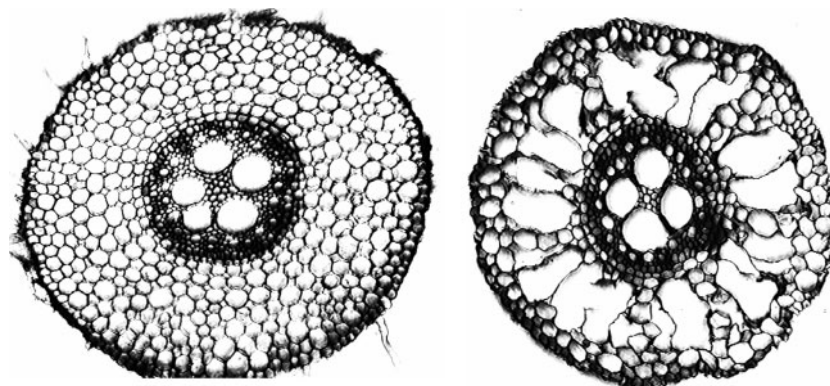

Fig. 9. Cross-sections of seminal roots of maize, showing genotypic difference in cortical aerenchyma formation, which replaces living cortical cells (left) with air-filled lacunae (right). Genotypes are closely related progeny (recombinant inbred lines) of the same two parents.
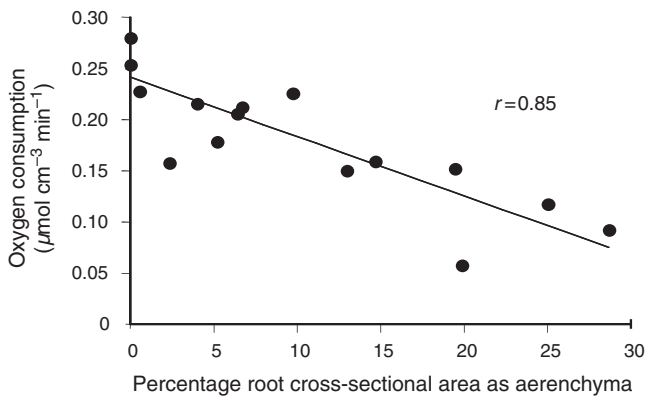
Fig. 10. Correlation between aerenchyma area and respiration in maize (*Zea mays* L.) roots. Each data point is the mean of six measurements of respiration and 10–12 measurements of aerenchyma on comparable root segments (Fan *et al*. 2003).
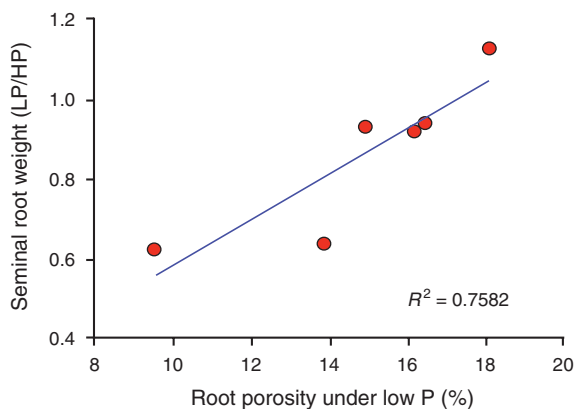

Fig. 11. Maintenance of root growth in a low-phosphorus (LP) field as related to formation of cortical aerenchyma in unrelated maize (*Zea mays* L.) genotypes. Root weights are expressed as the proportion of corresponding high-phosphorus (HP) roots. Each point is the mean of four replicates.

ease by which these molecules can be studied and manipulated through modern techniques in molecular and cellular biology, as well as the hope that their manipulation may be useful for improving plant adaptation to soil constraints, has led to considerable research that cannot be adequately summarised here (e.g. White 2000; Palmgren 2001; Very and Sentenac 2003; Raghothama and Karthikeyan 2005; Martinez-Ballesta *et al*. 2006).

In considering how manipulation of ion transporters may be useful in the Second Green Revolution, it is important to note that ion transport across membranes is not always a rate-limiting process in nutrient acquisition. Root uptake of nutrients whose movement in the soil is typically limited by diffusion, including ammonium, phosphate and potassium (Barber 1995), creates depletion zones near the root that have reduced nutrient availability. Mechanistic models predict that increasing the number of transporters (reflected in increased V_{max} of nutrient uptake) or their substrate affinity (reflected in decreased k_m for nutrient uptake) should have little effect on net acquisition of

phosphate, ammonium or potassium across time, because the activity of the transporters is limited by the arrival of new substrate at the root surface via the slow process of diffusion (Barber 1995). The activity of ion transporters may also be limited by the bioavailability of their substrate in soil. This is especially true for phosphate, which may be intercepted by many living and non-living soil constituents before it arrives at the root surface. In this case, altering ion transporters without improving substrate bioavailability (through such means of exudates) is not likely to improve net uptake. A third factor is leakage of acquired ions from the root back into the soil, which is especially important when an ion faces a strongly unfavourable electrochemical gradient for uptake across the plasma membrane (Britto and Kronzucker 2006). For example, at realistic phosphate concentrations, phosphate efflux is up to 80% of phosphate influx in maize roots (Elliott *et al*. 1984). Aggressive re-acquisition of leaked ions by modified transporters may only waste metabolic energy. Therefore, there are various reasons why manipulation of ion transporters, although technically feasible, may have limited utility in the second Green Revolution.

Manipulation of ion transport properties is expected to be useful in improving the acquisition of nutrients that are carried to the root by mass flow of water, including nitrate, calcium and magnesium. Nitrate transporters should have a role in efficient nitrate acquisition (Forde 2000; Britto and Kronzucker 2004). Modelling studies suggest that the V_{max} of nitrate transport at the root surface, which could be changed by increasing the copy number of nitrate transporters, should enhance nitrate acquisition (Barber 1995). Since a large part of the economic and environmental cost of intensive crop production is related to the production and use of nitrogen fertilisers, the production of crop genotypes with increased nitrogen efficiency is of interest to the agricultural biotech industry. Selection of crops with superior calcium and magnesium transport characteristics would be useful in acid soils of the humid tropics. Ion transporters may be also useful in improving the acquisition of metals, such as iron, zinc and manganese, present in low concentrations in certain soils (Rengel 2001; Ramesh *et al*. 2004; Broadley *et al*. 2007). Manipulation of ion transporters may be especially useful for improving crop tolerance to salinity, by enhancing exclusion or compartmentalisation of toxic ions (Blumwald *et al*. 2000; Munns *et al*. 2002).

Microbial symbioses

The majority of higher plant species have mycorrhizal symbioses with fungi that assist nutrient acquisition (Smith and Read 1997). Ectomycorrhizas enhance phosphorus acquisition via mobilisation of sparingly soluble phosphorus, whereas both ectomycorrhizas and arbuscular mycorrhizas common in many annuals and hardwood species enhance phosphorus acquisition by increasing the volume of soil explored beyond the depletion zone surrounding the root. In exchange for phosphorus, the plant provides the fungal symbiont with reduced carbon. The carbon cost of mycorrhizal symbioses can be a significant component of the metabolic cost of phosphorus acquisition. In bean, mycorrhizal colonisation increased root phosphorus acquisition, but the resulting increase in shoot photosynthesis
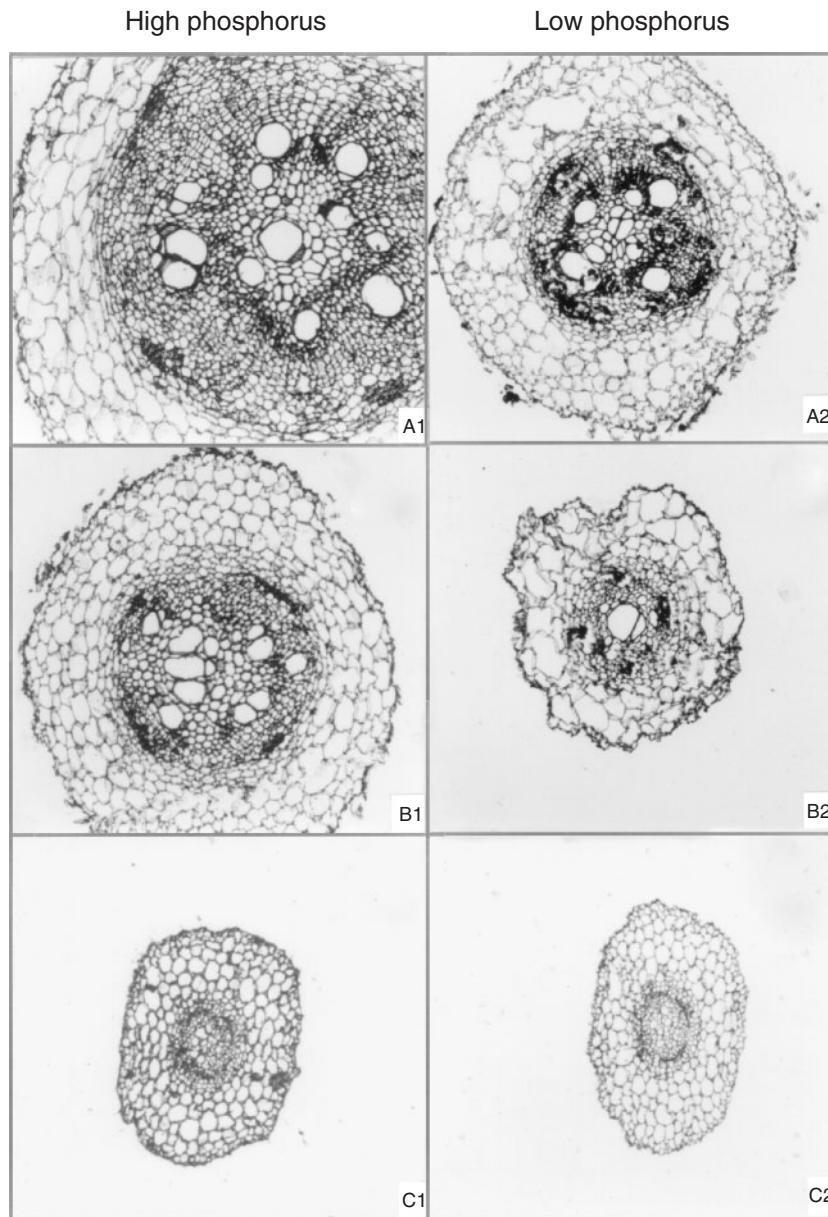
High phosphorus   Low phosphorus

Fig. 12. Retarded secondary development ('root etiolation') of basal roots of common bean in response to low phosphorus availability. Left panel: high phosphorus availability; right panel: low phosphorus availability. Top panels (A1 and A2), basal portion of the root; middle panels (B1 and B2), middle portion of the root; bottom panels (C1 and C2), apical portion of the root. Data are from Fan *et al*. (2003).

did not result in increased plant growth because of greater root respiration (Nielsen *et al*. 1998). At high phosphorus supply, mycorrhizal colonisation reduced the growth of citrus seedlings because of greater root carbon cost (Peng *et al*. 1993). In general, the cost 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 phosphorus acquisition has lead some mycorrhizal researchers to the belief that root traits are secondary or trivial in importance for phosphorus acquisition compared with fungal-assisted phosphorus acquisition. In this context, it is useful to consider the strong correlations observed between phosphorus uptake and root traits such as root-hair length (Miguel 2004, 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,
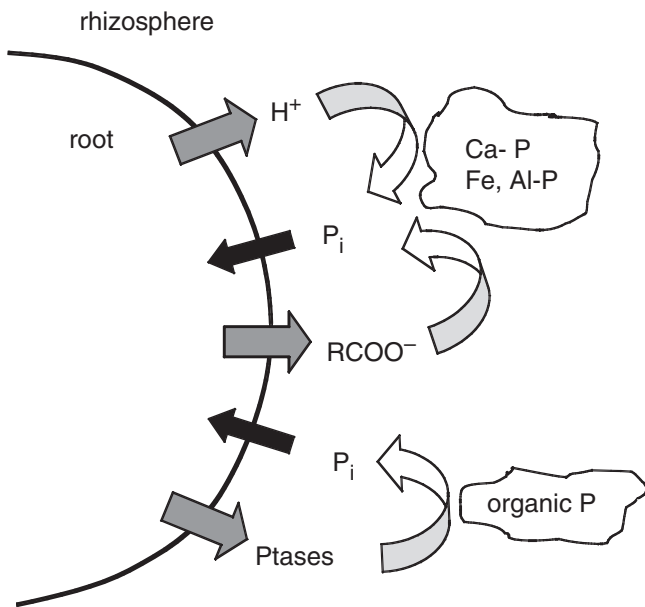
Fig. 13. Simplified diagram of the role of root exudates in phosphorus solubilisation in the rhizosphere. Protons and carboxylate anions (citrate and malate are important carboxylate exudates in many species) solubilise phosphate from metal complexes and enhance phosphate desorption from metal oxide surfaces. Protons are particularly important for phosphate solubilisation from calcium complexes in alkaline soils. Phosphatase enzymes can release phosphate from organic compounds. Rhizosphere microorganisms also produce phosphorus-solubilising exudates.

or that extraradical hyphae are restricted to the volume of soil near the root (Owusu-Bennoah and Wild 1979), so that root architectural patterns have a strong influence on foraging patterns by the fungal symbiont. Genetic variation exists in maize for mycorrhizal colonisation, controlled by several QTL (Kaeppler *et al*. 2000). Genotypic variation in mycorrhizal responsiveness among crop genotypes is associated with reduced expression of root traits responsible for fine-scale foraging such as root hairs or fine branching, resulting in a functional compensation of mycorrhizal and root traits (Koide 2000). In maize, soybean and common bean, genotypic rankings for plant growth in low-phosphorus soil in the field where mycorrhizas are formed are similar to genotypic rankings in controlled environments without mycorrhizas (e.g. 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 but does not represent a selection criterion (either through natural selection or in plant breeding) among genotypes, possibly because it is virtually ubiquitous.

Root symbioses and associations with bacteria capable of fixing nitrogen from the air are critically important for nitrogen input to agroecosystems. Biological nitrogen fixation has been the subject of a huge scientific effort over several decades (Vance 2002; Sprent 2005). Genetic variation exists for host-plant ability to exploit both symbiotic and associative fixation, which could be quite useful for improving the productivity and sustainability of low-input agroecosystems (Ladha and Peoples

1995; Hardarson and Broughton 2003). Biological nitrogen fixation in low-fertility environments is often limited by the availability of phosphorus, calcium and aluminum (Marschner 1995; Vance *et al*. 2000). Thus, legume genotypes with superior ability to acquire calcium and phosphorus, and tolerate high aluminum availability, may afford additional benefit in the form of enhanced nitrogen fixation. In strongly acid soils, however, increased nitrogen fixation may be counterproductive, as nitrogen fixation and nitrate leaching accelerate soil acidification and the leaching of calcium, magnesium and potassium, which may be more critical limitations than nitrogen itself (Marschner 1995).

Breeding issues

Routine field screening of large numbers of genotypes for low-fertility adaptation is generally noisy, costly, slow and unproductive (e.g. Singh *et al*. 1989). There are several reasons for this, including (1) large spatial variation in soil properties, especially when the topography is not completely flat, (2) subsoil acidity and compaction, which can restrict root growth, (3) the fact that most experiment stations are located on fertile soil, (4) confounding effects of past management practices on soil fertility, especially residual effects of lime and phosphorus application, (5) confounding effects of environmental interactions, including light and precipitation that can influence stress severity (effects which are especially problematic for manganese toxicity, Gonzalez *et al*. 1998), (6) the difficulty of isolating specific edaphic stresses from other co-occurring stresses, as is the case for example with the acid soil complex, where aluminum toxicity is difficult to separate from deficiency of phosphorus, calcium, magnesium and potassium, (7) confounding effects of biotic stresses, especially those that affect roots such as nematodes and root rots, (8) the difficulty of directly evaluating root phenotypes in the field and (9) the statistical improbability of identifying genotypes possessing useful traits in a setting in which the possession of many distinct, yet interacting, traits is necessary for organismal success.

This last point is especially relevant considering that much of the crop breeding that has occurred in the past 50 years has focused on yield traits and disease resistance, selected under high fertility. Most of the elite lines that are now being used as parents in crossing programs may therefore have little adaptation to low-fertility soils. In contrast, landraces have undergone centuries of selection with low inputs, and may have many useful traits, but may lack disease resistance, local adaptation, high yield, grain marketability or other traits that are important for success in field trials. For example, a genotype possessing root traits enabling superior phosphorus acquisition but that cannot efficiently mobilise that phosphorus to grain because of indeterminacy or late maturity will not be identified as a source of useful traits in a yield trial.

A better strategy is to follow the proven methods used in breeding for tolerance of biotic stress, which are to evaluate a wide range of germplasm for the expression of specific tolerance traits to specific disease/pest organisms, in many cases specific races or variants of pathogens. Once genotypes that have useful traits for specific stresses are identified, they are

incorporated into a crossing program to integrate these traits with other desirable traits such as high yield, marketability, and so on, for specific regions. Similarly, trait-based selection for specific edaphic stresses is much more likely to be successful than simple screening of elite lines for growth or yield in infertile soil. Although some traits such as aluminum tolerance have manifold benefits for nutrient capture by sustaining root growth, many other traits of interest may only have value for specific stresses. For example, manganese tolerance involves leaf antioxidant mechanisms (Gonzalez *et al.* 1998) that have little direct impact on aluminum tolerance or phosphorus acquisition, and traits enhancing the acquisition of immobile resources such as phosphorus and potassium may have little direct benefit for the acquisition of mobile resources such as nitrate or magnesium. Traits identified for selection should ideally be clearly defined and genetically distinct. For example, root depth is an aggregate of several traits under distinct genetic control, as discussed above, and is therefore not a distinct trait *per se*. The use of clearly defined, distinct traits improves the genetic precision of a selection program and also in many cases may permit the use of rapid screens. For example, root angles measured in 5-day-old bean seedlings in plastic bags are well correlated with root shallowness in field trials, and indeed with seed yield under low phosphorus (Fig. 5*b*, Bonser *et al.* 1996).

For a trait-based selection to be effective, we need a better understanding of the biology of these traits, how they contribute to fitness in the context of other traits, and the potential ecophysiological tradeoffs they may entail. For example, although the length and density of root hairs individually contribute to phosphorus acquisition, the expression of both of these traits together is strongly synergistic, contributing 290% more to phosphorus acquisition than would be predicted by their additive contributions (Ma *et al.* 2001*b*). Antagonistic interactions among traits are also possible, such as the placement of long root hairs in infertile soil domains by deep basal roots. The large genotypic variation for root traits suggests that their value may vary in distinct environments. For example, although shallow-rooted genotypes of bean have superior phosphorus acquisition, deep-rooted genotypes are more drought-tolerant (Fig. 14, Ho *et al.* 2004, 2005). Since many bean production environments are characterised by both drought and low phosphorus, this tradeoff should be reconciled before the selection of shallow root traits in bean breeding. Another common tradeoff is that biomass allocation to one root class may reduce growth of another root class because of assimilate competition (Walk *et al.* 2006).

An advantage of trait-based selection rather than yield selection is that a wide variety of exotic materials can be evaluated regardless of their environmental adaptation. Landraces and wild crop relatives from extreme soil environments may be particularly good sources of useful traits. For example, a soil-oriented core collection was used to identify phosphorus-efficient landraces of bean from low-fertility highlands (Beebe *et al.* 1997), and wild *Phaseolus* relatives native to saline deserts of Mexico were identified as potential sources of salt tolerance for bean breeding (Bayuelo-Jimenez *et al.* 2002*a*, 2002*b*, 2003).

Recent advances in the availability of well developed molecular genetic maps (Senior *et al.* 1996) and the definition
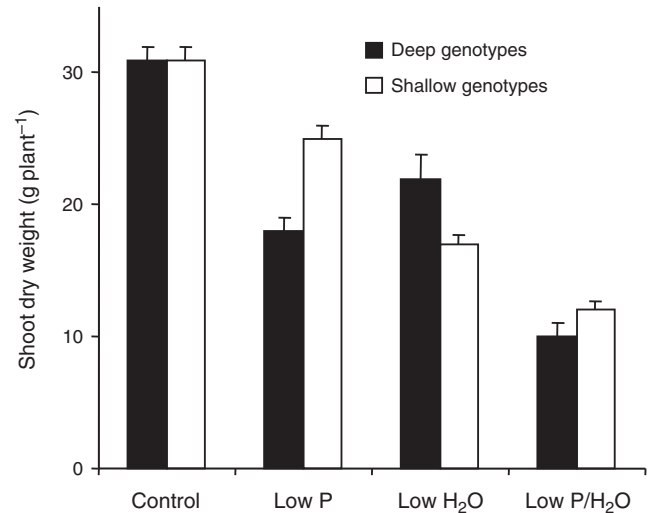

Fig. 14. Root architectural tradeoffs for acquisition of water and phosphorus. Data are for common bean genotypes grown in the field in Honduras at 44 days after planting. Three deep-rooted genotypes were compared with three shallow-rooted genotypes with the same genetic background, exposed to low phosphorus availability, terminal drought or drought and low phosphorus availability combined. Bars show the mean of 15 measurements (three genotypes replicated five times) $\pm$ s.e. Deep- and shallow-rooted genotypes had significantly different biomass under each stress regime (for low P: $F = 43.2$, $P = 0.003$; for drought: $F = 15.9$, $P = 0.016$; for combined drought and low P: $F = 8.4$, $P = 0.044$). Data are from Ho *et al.* (2005).

of distinct root traits for soil adaptation make it possible to identify and locate genes or quantitative trait loci (QTL) for root traits. Since root traits can be difficult to evaluate, they are good candidates for marker-assisted selection, whereby molecular markers linked to reliable QTL are selected as a substitute for phenotypic evaluation. Marker assisted selection may be especially useful to pyramid multiple traits, such as adventitious rooting, acid exudation, root hair density, mycorrhizal responsiveness and basal root gravitropism, all of which are associated with main effect QTL (Kaeppler *et al.* 2000; Tuberosa *et al.* 2002; Liao *et al.* 2004; Yan *et al.* 2004; Mano *et al.* 2005; Zhu *et al.* 2005*a*, 2005*b*, 2006; Ochoa *et al.* 2006).

System impacts

The utility of root traits for soil adaptation will be manifest in competitive environments, in subsistence agroecosystems usually in mixed stands with diverse taxa, and in commercial agriculture typically in high-density genetic monocultures. Obviously, traits influencing soil adaptation will affect plant productivity, and thereby competitive performance, under edaphic stress. An example of this is the positive effect of root hairs on plant competitiveness in mixed stands of *Arabidopsis* at low phosphorus but not at high phosphorus availability (Bates and Lynch 2001). Traits influencing nutrient acquisition can also directly affect interplant competition by removing soil resources that could be accessed by competitors. For example, bean genotypes with shallow basal roots outcompete genotypes with deep basal roots in low-phosphorus fields (Rubio *et al.*

2003), because of enhanced topsoil exploitation and reduced competition (i.e. reduced overlap of phosphorus-depletion zones) 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 nutrient acquisition. This appears to be the case for plasticity of basal-root shallowness, for which genetic variation exists; i.e. some genotypes respond to phosphorus stress by becoming more shallow, whereas others are unaffected or become deeper (Bonser *et al.* 1996; Ho *et al.* 2004, 2005). Plasticity of root shallowness would generally be considered to be 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. Modelling showed that interplant competition could be important in determining an optimal balance of plastic and non-plastic root phenotypes under conditions of phosphorus stress and combined phosphorus and water stress (Fig. 15; Ho 2004). This suggests that genetic mixtures or multilines may have better performance in low-phosphorus agroecosystems than do genetic monocultures, especially in drought-prone environments.

The development of crops with superior growth in low-fertility soil and with better responsiveness to applied fertiliser inputs would have tremendous value in many developing countries, where yields are limited by low soil fertility and
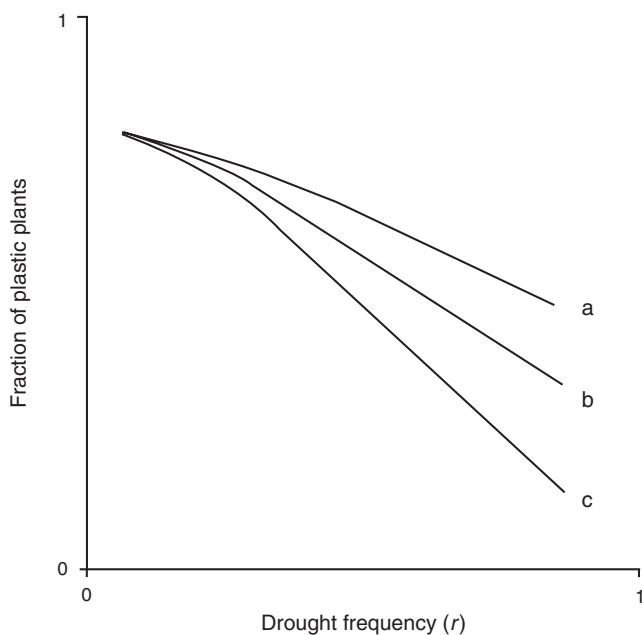
fertiliser use is minimal (Lynch 1998). Since genotypic variation for nutrient acquisition efficiency is much larger than variation for nutrient use efficiency in crop plants, it is likely that nutrient-efficient crops will have greater nutrient acquisition than do conventional genotypes. Although such genotypes would extract more nutrients from the soil than conventional genotypes, they may actually enhance soil fertility in the 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 1998; Lynch and Deikman 1998). This is especially true for legumes, since enhanced growth of legumes benefits the cropping system by increasing biological nitrogen fixation. Indeed, given the importance of legumes for nitrogen availability and human nutrition, and their high market value compared with staple crops, improving the phosphorus efficiency and aluminum tolerance of legumes would have manifold benefits for the third-world agriculture (Vance 2001).

Of the three main components of integrated nutrient management (fertility inputs, soil management and adapted germplasm), adapted germplasm is arguably the leading edge of improved productivity for poor farmers. Valued seed is typically freely shared by farm communities, and requires no additional investment of capital, expertise, time or labour for resource-poor farmers. Increased yields from adapted germplasm would enhance household nutrition and income, permitting farmers to afford fertility inputs, education for their children and other investments to help them climb out of a vicious cycle of low inputs, low yields and environmental degradation.

Nutrient-efficient crops would be useful in wealthy nations by reducing the cost of production and environmental impacts of intensive fertilisation (Lynch 1998). The price of nitrogen fertilisers has increased substantially in recent years along with the price of energy (primarily natural gas), since industrial N fixation is energy-intensive. The devastating effects of fertiliser runoff on aquatic ecosystems are evident in the alarming spread of 'dead zones' surrounding the outlets of rivers such as the Mississippi (Rabalais *et al.* 2002).

The case of phosphorus efficiency in bean and soybean

As an example of the potential of the second Green Revolution, I will summarise research with adaptation to low phosphorus availability ('phosphorus efficiency') in common bean. As with most tropical crops, low phosphorus availability is a primary constraint to bean production, affecting well over half of tropical production (Table 2). Substantial genetic variation exists in bean germplasm for phosphorus efficiency, but 20 years of field screening in low-fertility soil had failed to identify materials superior to 'Carioca', a landrace adapted to the low-phosphorus soils of Brazil (Singh *et al.* 1989). In 1987, we initiated a more focused, trait-oriented approach to this problem by evaluating a common set of genotypes in contrasting soils in the field, and with contrasting phosphorus substrates under controlled conditions. The genetic ranking for phosphorus efficiency was largely unchanged by the soil type, phosphorus substrate or mycorrhizal status, indicating that in this species, plant-specific factors rather than rhizosphere interactions accounted for genotypic variation in phosphorus efficiency (Yan *et al.* 1995*a*,

Fig. 15. Results of a theoretical model, showing that there is an optimum mixture of plastic (i.e. plants capable of forming shallower roots under low phosphorus availability) and non-plastic (i.e. plants maintaining a deep root architecture regardless of phosphorus availability) plants in a population, which varies depending on the frequency and severity of drought. Curves a–c represent increasing drought severity. Data are from Ho (2004).

1995*b*, 1996). We observed large genetic variation for root growth and architecture in bean (Lynch and van Beem 1993) and hypothesised that these differences accounted for genotypic variation in phosphorus efficiency (Lynch and Beebe 1995). Knowing that root traits were of interest, we developed field research sites with uniform, low phosphorus availability but without other nutritional problems or constraints to root growth, including subsoil acidity and compaction. On these sites, we screened a soil-oriented core collection of 364 bean genotypes, representing a broad sampling of the genetic diversity of *Phaseolus vulgaris*, with an emphasis on landraces from regions identified as having low-fertility soils (Beebe *et al*. 1997). This survey identified several landraces with outstanding phosphorus efficiency. More thorough sampling of germplasm from these regions resulted in identification of landraces with superior phosphorus efficiency compared with Carioca (Fig. 16). These landraces are now being employed in breeding programs in Africa and Latin America. These genotypes also became useful research tools to understand the physiological and genetic basis of phosphorus efficiency in this species. Populations (recombinant inbred lines or RILs) developed from crosses of phosphorus-efficient and phosphorus-inefficient parents have permitted physiological and genetic analyses of genotypes with contrasting phosphorus efficiency but with the same genetic background. Studies with these genotypes identified several distinct root traits that contribute to phosphorus efficiency in this species, including root-hair length and density (Miguel 2004; Yan *et al*. 2004), adventitious rooting (Miller *et al*. 2003; Ochoa *et al*. 2006), basal-root shallowness (Bonser *et al*. 1996; Liao *et al*. 2001; Liao *et al*. 2004) and traits that reduce the metabolic costs of root maintenance, such as root etiolation and root cortical aerenchyma (Fan *et al*. 2003; Lynch and Ho

2005). Several of these traits can be evaluated in rapid screens with young plants, greatly facilitating breeding and selection. These traits are now being used as selection criteria for bean breeding for low-fertility soils of eastern Africa. These traits have also been used as an idiotype to guide the development of phosphorus-efficient soy genotypes for South China (Yan 2005), which has resulted in the release of five new commercial lines with substantially greater yield in low-phosphorus soils, with 10 more in the final stages of multilocational evaluation before release. Several of these traits are also important for phosphorus efficiency in maize (Fan *et al*. 2003; Zhu and Lynch 2004; Zhu *et al*. 2005*a*, 2005*b*, 2005*c*, 2006) and we anticipate that they will be useful in most annual crops.

Prospects

The second Green Revolution is underway. The development of soybean, wheat and maize genotypes tolerant of acid, infertile soils is a critical component of the technology package developed by EMBRAPA that has successfully converted large areas of the Brazilian Cerrado to crop cultivation. Breeders at the CGIAR centres, including CIMMYT, IRRI, CIAT and ICRISAT, are increasingly incorporating soil adaptation as an explicit element of their selection programs. Recent progress in elucidating the physiological and genetic basis of aluminum tolerance in crops is likely to lead to significant practical impacts across the next 10 years. Progress in identifying specific root traits that enhance nutrient acquisition has had a significant impact on breeding bean and soybean genotypes that have superior growth in low-phosphorus soils. The explosion of genomics information has created opportunities for understanding and exploiting the large genetic variation present in crop species for soil adaptation. We are poised to make a very significant contribution to food security in developing nations.

However, we face several obstacles in achieving this goal. Few stakeholders are aware of the potential to develop crops with tolerance to low-fertility soils, and this is reflected by low prioritisation of this activity in national research programs (especially in the USA), international development efforts, and professional training. This is puzzling, considering the central importance of soil fertility in agricultural production in developing nations, the serious environmental problems caused by overfertilisation in rich countries, decades of research documenting large genetic variation within crop species for soil adaptation, and the example of the first Green Revolution, which was based on plant adaptation to soil fertility. There are several factors that may contribute to this paradoxical neglect. One is that most research is conducted by and for rich countries, especially in Western Europe and the USA, which generally have fertile soils and (historically) inexpensive fertilisers. Some of the most significant research on this topic is increasingly being conducted by nations with more problematic soils, such as China, Australia and Brazil (e.g. Yan *et al*. 2006). Another problematic factor is disciplinary specialisation, since this topic involves the interface of soil science and plant biology. In this context, the existence of institutes devoted to plant nutrition (or even 'Nutriomics'), notably in Germany, China and Australia, is important in ensuring a future for rigorous research and training on the interface of plants and soils. A related factor is the dominance
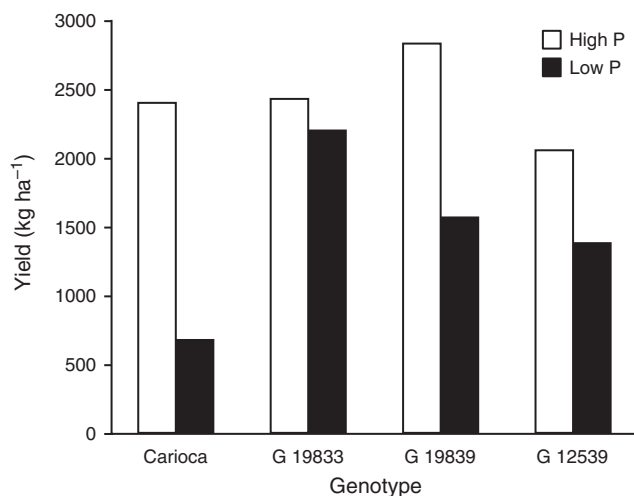

Fig. 16. Genotypic variation for phosphorus efficiency in common bean (*Phaseolus vulgaris*) grown in low-phosphorus soils of Colombia. Mass screening for yield in low-fertility soils failed to identify genotypes with superior phosphorus efficiency compared with the Brazilian landrace Carioca. After targeted germplasm sampling and root phenotyping, landraces were identified with superior phosphorus efficiency compared with Carioca, including the lines shown here. Data provided by Steve Beebe, CIAT.

of plant pathology, which historically has de-emphasised abiotic stresses, in the training of plant breeders. An overarching problem is the monopolisation of research and training budgets by molecular biology and its recent incarnations (e.g. genomics, proteomics), with an attendant focus on model organisms. This has widened the gap between applied and basic research, and also has created a funding and training vacuum for the biology of organs, organisms and organism–environment interactions, which we need to understand better in order to exploit complex traits such as root growth and architecture. As yet, molecular approaches have been more useful for single-gene traits rather than for the complex quantitative genetics and substantial intraspecific variation typical of many root traits. Another overarching problem is the low esteem in which agricultural research is held by many plant biologists, including reviewers of grant proposals, thesis proposals and manuscripts submitted for publication in prestigious journals. Considering that plant biologists justify public investment in plant research with the implicit and explicit promise to deliver public benefits, and the potential cost of lives lost in the third world because of delays in agricultural innovation, the disdain of elite plant biologists for agricultural research is difficult to rationalise from an ethical perspective. Unfortunately, these factors are creating a situation in which expanding opportunities to realise the benefits of a second Green Revolution are being met by a global plant nutrition research effort that is sparse, uneven, and threatened by dwindling support.

The confluence of a growing world population, ongoing land degradation, rising fuel and therefore fertiliser costs, dwindling supplies of high-grade phosphorus ore (Abelson 1999) and the uncertain effects of global climate change in low-fertility environments (Lynch and St Clair 2004) will ensure that the need for a second Green Revolution will only increase in coming decades. Will we rise to this challenge?

Acknowledgements

References

Abel S, Ticconi CA, Delatorre CA (2002) Phosphate sensing in higher plants. *Physiologia Plantarum* **115**, 1–8.
doi: 10.1034/j.1399-3054.2002.1150101.x

Abelson P (1999) A potential phosphate crisis. *Science* **283**, 2015.
doi: 10.1126/science.283.5410.2015

Ali MY, Krishnamurthy L, Saxena NP, Rupela OP, Kumar J, Johansen C (2002) Scope for genetic manipulation of mineral acquisition in chickpea. *Plant and Soil* **245**, 123–134. doi: 10.1023/A:1020616818106

Anonymous (1887) Report of the Pennsylvania State College Agricultural Experimental Station. Official Document Number 13, University Park, PA, USA.

Barber SA (1995) 'Soil nutrient bioavailability: a mechanistic approach.' (John Wiley & Sons Inc.: New York)

Bates TR, Lynch JP (1996) Stimulation of root hair elongation in *Arabidopsis thaliana* by low phosphorus availability. *Plant, Cell & Environment* **19**, 529–538. doi: 10.1111/j.1365-3040.1996.tb00386.x

Bates T, Lynch JP (2000*a*) Plant growth and phosphorus accumulation of wild type and two root hair mutants of *Arabidopsis thaliana* (Brassicaceae). *American Journal of Botany* **87**, 958–963.
doi: 10.2307/2656994

Bates T, Lynch JP (2000*b*) The efficiency of *Arabidopsis thaliana* (Brassicaceae) root hairs in phosphorus acquisition. *American Journal of Botany* **87**, 964–970. doi: 10.2307/2656995

Bates T, Lynch JP (2001) Root hairs confer a competitive advantage under low phosphorus availability. *Plant and Soil* **236**, 243–250.
doi: 10.1023/A:1012791706800

Baumhardt RL, Tolk JA, Winter SR (2005) Seeding practices and cultivar maturity effects on simulated dryland grain sorghum yield. *Agronomy Journal* **97**, 935–942. doi: 10.2134/agronj2004.0087

Bayuelo-Jimenez JS, Craig R, Lynch JP (2002*a*) Salinity tolerance of *Phaseolus* species during germination and early seedling growth. *Crop Science* **42**, 1584–1594.

Bayuelo-Jimenez JS, Debouck DG, Lynch JP (2002*b*) Salinity tolerance in *Phaseolus* species during early vegetative growth. *Crop Science* **42**, 2184–2192.

Bayuelo-Jimenez JS, Debouck DG, Lynch JP (2003) Growth, gas exchange, water relations, and ion composition of *Phaseolus* species grown under saline conditions. *Field Crops Research* **80**, 207–222.
doi: 10.1016/S0378-4290(02)00179-X

Beaver JS, Rosas JC, Myers J, Acosta J, Kelly JD, Nchimbi-Msolla S, Misangu R, Bokosi J, Temple S, Arnaud-Santana E, Coyne DP (2003) Contributions of the bean/cowpea CRSP to cultivar and germplasm development in common bean. *Field Crops Research* **82**, 87–102.
doi: 10.1016/S0378-4290(03)00032-7

Beebe S, Lynch JP, Galwey N, Tohme J, Ochoa I (1997) A geographical approach to identify phosphorus-efficient genotypes among landraces and wild ancestors of common bean. *Euphytica* **95**, 325–336.
doi: 10.1023/A:1003008617829

Bhat KKS, Nye PH (1974) Diffusion of phosphate to plant roots in soil. III. Depletion around onion roots without root hairs. *Plant and Soil* **41**, 383–394. doi: 10.1007/BF00017265

Bloom AJ, Chapin FSI, Mooney HA (1985) Resource limitation in plants—an economic analogy. *Annual Review of Ecology and Systematics* **16**, 363–392.

Blumwald E, Aharon GS, Apse MP (2000) Sodium transport in plants. *Biochimica et Biophysica Acta* **1465**, 140–151.
doi: 10.1016/S0005-2736(00)00135-8

Bonser AM, Lynch JP, Snapp S (1996) Effect of phosphorus deficiency on growth angle of basal roots in *Phaseolus vulgaris*. *New Phytologist* **132**, 281–288. doi: 10.1111/j.1469-8137.1996.tb01847.x

Borch K, Bouma TJ, Lynch JP, Brown KM (1999) Ethylene: a regulator of root architectural responses to soil phosphorus availability. *Plant, Cell & Environment* **22**, 425–431.
doi: 10.1046/j.1365-3040.1999.00405.x

Borlaug NE (1972) The green revolution, peace, and humanity. In 'Speech delivered upon receipt of the 1970 Nobel Peace Prize'. (Centro Internacional de Mejoramiento de Maiz y Trigo: El Batan, Mexico)

Bouldin D (1961) Mathematical description of diffusion process in the soil. *Soil Science Society of America Proceedings* **25**, 476–480.

Bouranis DL, Chorianopoulou SN, Siyiannis VF, Protonotarios VE, Hawkesford MJ (2003) Aerenchyma formation in roots of maize during sulphate starvation. *Planta* **217**, 382–391.
doi: 10.1007/s00425-003-1007-6

Britto D, Kronzucker H (2004) Bioengineering nitrogen acquisition in rice: can novel initiatives in rice genomics and physiology contribute to global food security? *BioEssays* **26**, 683–692. doi: 10.1002/bies.20040

Britto D, Kronzucker H (2006) Futile cycling at the plasma membrane: a hallmark of low-affinity nutrient transport. *Trends in Plant Science* **11**, 529–534. doi: 10.1016/j.tplants.2006.09.011

Broadley MR, White PJ, Hammond JP, Zelko I, Lux A (2007) Zinc in plants. *New Phytologist* **173**, 677–702. doi: 10.1111/j.1469-8137.2007.01996.x

Caradus J (1981) Effect of root hair length on white clover growth over a range of soil phosphorus levels. *New Zealand Journal of Agricultural Research* **24**, 359–364.

Chrispeels MJ, Crawford NM, Schroeder JI (1999) Proteins for transport of water and mineral nutrients across the membranes of plant cells. *The Plant Cell* **11**, 661–675. doi: 10.1105/tpc.11.4.661

Clarkson DT (1985) Factors affecting mineral acquisition by plants. *Annual Review of Plant Physiology* **36**, 77–115. doi: 10.1146/annurev.pp.36.060185.000453

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 Physiology* **86**, 491–496.

Drew MC, Saker LR (1978) Nutrient supply and the growth of the seminal root system in barley. *Journal of Experimental Botany* **29**, 435–451. doi: 10.1093/jxb/29.2.435

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 Physiology* **91**, 266–271.

Dunbabin V, Diggle A, Rengel Z (2003) Is there an optimal root architecture for nitrate capture in leaching environments? *Plant, Cell & Environment* **26**, 835–844. doi: 10.1046/j.1365-3040.2003.01015.x

Eissenstat DM, Graham JH, Syvertsen JP, Drouillard DL (1993) Carbon economy of sour orange in relation to mycorrhizal colonization and phosphorus status. *Annals of Botany* **71**, 1–10. doi: 10.1006/anbo.1993.1001

Elliott GC, Lynch JP, Lauchli A (1984) Influx and efflux of P in roots of intact maize plants. Double-labeling with ^{32}P and ^{33}P. *Plant Physiology* **76**, 336–341.

Esau K (1977) 'Anatomy of seed plants.' (John Wiley and Sons: New York)

Eshel A, Nielsen K, Lynch JP (1995) Response of bean root systems to low level of P. In 'Plant roots—from cells to systems. 14th Long Ashton international symposium'. p. 63. (IACR–Long Ashton Research Station: Bristol, England)

Fan MS, Zhu JM, Richards C, Brown KM, Lynch JP (2003) Physiological roles for aerenchyma in phosphorus-stressed roots. *Functional Plant Biology* **30**, 493–506. doi: 10.1071/FP03046

FAO (2002) 'The state of food insecurity in the world 2002.' (The Food and Agriculture Organisation of the United Nations: Rome)

Fitter A, Williamson L, Linkohr B, Leyser O (2002) Root system architecture determines fitness in an *Arabidopsis* mutant in competition for immobile phosphate ions but not for nitrate ions. *Proceedings of the Royal Society of London. Series B. Biological Sciences* **269**, 2017–2022. doi: 10.1098/rspb.2002.2120

Foehse 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 and Soil* **132**, 261–272.

Forde BG (2000) Nitrate transporters in plants: structure, function, and regulation. *Biochimica et Biophysica Acta* **1465**, 219–235. doi: 10.1016/S0005-2736(00)00140-1

Foy CD, Chaney RL, White MC (1978) The physiology of metal toxicity in plants. *Annual Review of Plant Physiology* **29**, 511–566. doi: 10.1146/annurev.pp.29.060178.002455

Gahoonia TS, Nielsen NE (1997) Variation in root hairs of barley cultivars doubled soil phosphorus uptake. *Euphytica* **98**, 177–182. doi: 10.1023/A:1003113131989

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 & Environment* **26**, 1759–1766. doi: 10.1046/j.1365-3040.2003.01093.x

Gahoonia TS, Nielsen NE (2004) Root traits as tools for creating phosphorus efficient crop varieties. *Plant and Soil* **260**, 47–57. doi: 10.1023/B:PLSO.0000030168.53340.bc

Gahoonia TS, Care D, Nielsen NE (1997) Root hairs and phosphorus acquisition of wheat and barley cultivars. *Plant and Soil* **191**, 181–188. doi: 10.1023/A:1004270201418

Gahoonia TS, Nielsen NE, Lyshede OB (1999) Phosphorus (P) acquisition of cereal cultivars in the field at three levels of P fertilization. *Plant and Soil* **211**, 269–281. doi: 10.1023/A:1004742032367

Gahoonia TS, Nielsen NE, Joshi PA, Jahoor A (2001) A root hairless barley mutant for elucidating genetic of root hairs and phosphorus uptake. *Plant and Soil* **235**, 211–219. doi: 10.1023/A:1011993322286

Ge ZY, 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 and Soil* **218**, 159–171. doi: 10.1023/A:1014987710937

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 Biotechnology Journal* **3**, 129–140. doi: 10.1111/j.1467-7652.2004.00116.x

Goldstein A (1992) Phosphate starvation inducible enzymes and proteins in higher plants. In 'Inducible plant proteins'. (Ed. JL Wray) pp. 25–44. (Cambridge University Press: Cambridge, UK)

Gonzalez A, Steffen KL, Lynch JP (1998) Light and excess manganese— implications for oxidative stress in common bean. *Plant Physiology* **118**, 493–504. doi: 10.1104/pp.118.2.493

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. *Australian Journal of Biological Sciences* **25**, 1169–1180.

Halsted M, Lynch JP (1996) Phosphorus responses of C-3 and C-4 species. *Journal of Experimental Botany* **47**, 497–505. doi: 10.1093/jxb/47.4.497

Hardarson G, Broughton WJ (Eds) (2003) 'Maximising the use of biological nitrogen fixation in agriculture.' Developments in plant and soil sciences. (Kluwer Academic Publishers, Food and Agricultire Organisation of the United Nations, International Atomic Energy Agency: Dordrecht, The Netherlands)

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

Hartemink AE (2003) 'Soil fertility decline in the tropics.' (CABI Publishing: Wageningen, The Netherlands)

Hinsinger P (2001) Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: a review. *Plant and Soil* **237**, 173–195. doi: 10.1023/A:1013351617532

Hinsinger P, Gobran GR, Gregory PJ, Wenzel WW (2005) Rhizosphere geometry and heterogeneity arising from root mediated physical and chemical processes. *New Phytologist* **168**, 293–303. doi: 10.1111/j.1469-8137.2005.01512.x

Ho MD (2004) Effects of root architecture, plasticity, and tradeoffs on water and phosphorus acquisition in heterogenous environments. PhD Thesis, Penn State University, University Park, PA.

Ho M, McCannon B, Lynch JP (2004) Optimization modeling of plant root architecture for water and phosphorus acquisition. *Journal of Theoretical Biology* **226**, 331–340. doi: 10.1016/j.jtbi.2003.09.011

Ho M, Rosas J, Brown K, Lynch JP (2005) Root architectural tradeoffs for water and phosphorus acquisition. *Functional Plant Biology* **32**, 737–748. doi: 10.1071/FP05043

Itoh S, Barber S (1983*a*) A numerical solution of whole plant nutrient uptake for soil root systems with root hairs. *Plant and Soil* **70**, 403–413. doi: 10.1007/BF02374895

Itoh S, Barber S (1983*b*) Phosphorus uptake by six plant species as related to root hairs. *Agronomy Journal* **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 Biology* **1**, 274–287.

Jakobsen I, Rosendahl L (1990) Carbon flow into soil and external hyphae from roots of mycorrhizal cucumber plants. *New Phytologist* **115**, 77–83. doi: 10.1111/j.1469-8137.1990.tb00924.x

Jones DL, Dennis PG, Owen AG, van Hees PAW (2003) Organic acid behavior in soils—misconceptions and knowledge gaps. *Plant and Soil* **248**, 31–41. doi: 10.1023/A:1022304332313

Jungk A (2001) Root hairs and the acquisition of plant nutrients from soil. *Journal of Plant Nutrition and Soil Science* **164**, 121–129. doi: 10.1002/1522-2624(200104)164:2<121::AID-JPLN121>3.0.CO;2-6

Kaeppler SM, Parke JL, Mueller SM, Senior L, Stuber C, Tracy WF (2000) Variation among maize inbred lines and detection of quantitative trait loci for growth at low phosphorus and responsiveness to arbuscular mycorrhizal fungi. *Crop Science* **40**, 358–364.

Khush G (1999) Green revolution: preparing for the 21st century. *Genome* **42**, 646–655. doi: 10.1139/gen-42-4-646

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

Kochian LV, Piñeros MA, Hoekenga OA (2005) The physiology, genetics and molecular biology of plant aluminum resistance and toxicity. *Plant and Soil* **274**, 175–195. doi: 10.1007/s11104-004-1158-7

Koide RT (2000) Functional complementarity in the arbuscular mycorrhizal symbiosis. *New Phytologist* **147**, 233–235. doi: 10.1046/j.1469-8137.2000.00710.x

Konings H, Verschuren G (1980) Formation of aerenchyma in roots of *Zea mays* in aerated solutions, and its relation to nutrient supply. *Physiologia Plantarum* **49**, 265–279. doi: 10.1111/j.1399-3054.1980.tb02661.x

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 Physiology* **41**, 1030–1037. doi: 10.1093/pcp/pcd029

Ladha JK, Peoples MB (Eds) (1995) Management of biological nitrogen fixation for the development of more productive and sustainable agricultural systems. *Plant and Soil* **174**, 1–286.

Lambers H, Atkin O, Millenaar FF (2002) Respiratory patterns in roots in relation to their functioning. In 'Plant roots, the hidden half'. (Eds Y Waisel, A Eshel, K Kafkaki) pp. 521–552. (Marcel Dekker, Inc.: New York)

Lewis DG, Quirk JP (1967) Phosphate diffusion in soil and uptake by plants. *Plant and Soil* **26**, 445–453. doi: 10.1007/BF01379565

Li L, Tang CX, Rengel Z, Zhang FS (2003) Chickpea facilitates phosphorus uptake by intercropped wheat from an organic phosphorus source. *Plant and Soil* **248**, 297–303. doi: 10.1023/A:1022389707051

Li SM, Li L, Zhang FS, Tang C (2004) Acid phosphatase role in chickpea/maize intercropping. *Annals of Botany* **94**, 297–303. doi: 10.1093/aob/mch140

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 and Soil* **232**, 69–79. doi: 10.1023/A:1010381919003

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. *Functional Plant Biology* **31**, 959–970. doi: 10.1071/FP03255

Lopez-Bucio J, de la Vega OM, Guevara-Garcia A, Herrera-Estrella L (2000a) Enhanced phosphorus uptake in transgenic tobacco plants that overproduce citrate. *Nature Biotechnology* **18**, 450–453. doi: 10.1038/74531

Lopez-Bucio J, Nieto-Jacobo MF, Ramirez-Rodriguez V, Herrera-Estrella L (2000b) Organic acid metabolism in plants: from adaptive physiology to transgenic varieties for cultivation in extreme soils. *Plant Science* **160**, 1–13. doi: 10.1016/S0168-9452(00)00347-2

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 (1998) The role of nutrient efficient crops in modern agriculture. In 'Nutrient use in crop production'. (Ed. Z Rengel) (Food Products Press: New York)

Lynch JP (2005) Root architecture and nutrient acquisition. In 'Nutrient acquisition by plants. An ecological perspective'. (Ed. H BassiriRad) (Springer-Verlag: Berlin)

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

Lynch JP, van Beem JJ (1993) Growth and architecture of seedling roots of common bean genotypes. *Crop Science* **33**, 1253–1257.

Lynch JP, Brown KM (1998) Root architecture and phosphorus acquisition efficiency in common bean. In 'Phosphorus in plant biology: regulatory roles in ecosystem, organismic, cellular, and molecular processes'. (Eds JP Lynch, J Deikman) (American Society of Plant Physiologists: Rockville, MD)

Lynch JP, Brown KM (2001) Topsoil foraging—an architectural adaptation of plants to low phosphorus availability. *Plant and Soil* **237**, 225–237. doi: 10.1023/A:1013324727040

Lynch JP, Brown KM (2006) Whole plant adaptations to low phosphorus availability. In 'Plant–environment interactions'. 3rd edn. (Ed. B Huang) (Taylor and Francis: New York)

Lynch JP, Deikman J (1998) 'Phosphorus in plant biology: regulatory roles in molecular, cellular, organismic, and ecosystem processes.' (American Society of Plant Physiologists: Rockville, MD)

Lynch JP, Ho M (2005) Rhizoeconomics: carbon costs of phosphorus acquisition. *Plant and Soil* **269**, 45–56. doi: 10.1007/s11104-004-1096-4

Lynch JP, St Clair S (2004) Mineral stress: the missing link in understanding how global climate change will affect plants in real world soils. *Field Crops Research* **90**, 101–115. doi: 10.1016/j.fcr.2004.07.008

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

Ma Z, Bielenberg DG, Brown KM, Lynch JP (2001a) Regulation of root hair density by phosphorus availability in *Arabidopsis thaliana*. *Plant, Cell & Environment* **24**, 459–467. doi: 10.1046/j.1365-3040.2001.00695.x

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 and Soil* **236**, 221–235. doi: 10.1023/A:1012728819326

Mano Y, Muraki M, Fujimori M, Takamizo T, Kindiger B (2005) Identification of QTL controlling adventitious root formation during flooding conditions in teosinte (*Zea mays* ssp. *huehuetenangensis*) seedlings. *Euphytica* **142**, 33–42. doi: 10.1007/s10681-005-0449-2

Marschner H (1995) 'Mineral nutrition of higher plants.' (Academic Press: London)

Martinez-Ballesta M, Silva C, Lopez-Berenguer C, Cabanero F, Carvajal M (2006) Plant aquaporins: New perspectives on water and nutrient uptake in saline environment. *Plant Biology* **8**, 535–546. doi: 10.1055/s-2006-924172

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

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. *Functional Plant Biology* **30**, 973–985. doi: 10.1071/FP03078

Mollier A, Pellerin S (1999) Maize root system growth and development as influenced by phosphorus deficiency. *Journal of Experimental Botany* **50**, 487–497. doi: 10.1093/jexbot/50.333.487

Munns R, Husain S, Rivelli AR, James RA, Condon AGT, Lindsay MP, Lagudah ES, Schachtman DP, Hare RA (2002) Avenues for increasing salt tolerance of crops, and the role of physiologically based selection traits. *Plant and Soil* **247**, 93–105. doi: 10.1023/A:1021119414799

Neumann G, Römheld V (2002) Root-induced changes in the availability of nutrients in the rhizosphere. In 'Plant roots: the hidden half'. (Eds Y Waisel, A Eshel, U Kafkafi) pp. 617–649. (Marcel Dekker: New York)

Newman E (1997) Phosphorus balance of contrasting farming systems, past and present. Can food production be sustainable? *Journal of Applied Ecology* **34**, 1334–1347. doi: 10.2307/2405251

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 Phytologist* **139**, 647–656. doi: 10.1046/j.1469-8137.1998.00242.x

Nielsen KL, Eshel A, Lynch JP (2001) The effect of phosphorus availability on the carbon economy of contrasting common bean (*Phaseolus vulgaris* L.) genotypes. *Journal of Experimental Botany* **52**, 329–339. doi: 10.1093/jexbot/52.355.329

Ochoa I, Blair M, Lynch JP (2006) QTL Analysis of adventitious root formation in common bean (*Phaseolus vulgaris* L.) under contrasting phosphorus availability. *Crop Science* **46**, 1609–1621. doi: 10.2135/cropsci2005.12-0446

van Oosterom EJ, Bidinge FR, Weltzien ER (2003) A yield architecture framework to explain adaptation of pearl millet to environmental stress. *Field Crops Research* **80**, 33–56. doi: 10.1016/S0378-4290(02)00153-3

Owusu-Bennoah E, Wild A (1979) Autoradiography of the depletion zone of phosphate around onion roots in the presence of vesicular-arbuscular mycorrhiza. *New Phytologist* **82**, 133–140. doi: 10.1111/j.1469-8137.1979.tb07567.x

Palmgren MG (2001) Plant plasma membrane H + -ATPases: powerhouses for nutrient uptake. *Annual Review of Plant Physiology and Plant Molecular Biology* **52**, 817–845. doi: 10.1146/annurev.arplant.52.1.817

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 Physiology* **101**, 1063–1071.

Peng S, Cassman KG, Virmani SS, Sheehy J, Khush GS (1999) Yield potential trends of tropical rice since the release of IR8 and the challenge of increasing rice yield potential. *Crop Science* **39**, 1552–1559.

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

Piñeros MA, Shaff JE, Manslank HS, Alves VMC, Kochian LV (2005) Aluminum resistance in maize cannot be solely explained by root organic acid exudation. A comparative physiological study. *Plant Physiology* **137**, 231–241. doi: 10.1104/pp.104.047357

Rabalais NN, Turner RE, Wiseman WJJ (2002) Gulf of Mexico hypoxia, A.K.A. 'The dead zone'. *Annual Review of Ecology and Systematics* **33**, 235–263. doi: 10.1146/annurev.ecolsys.33.010802.150513

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

Raghothama KG, Karthikeyan AS (2005) Phosphate acquisition. *Plant and Soil* **274**, 37–49. doi: 10.1007/s11104-004-2005-6

Ramesh SA, Choimes S, Schachtman DP (2004) Over-expression of an *Arabidopsis* zinc transporter in *Hordeum vulgare* increases short-term zinc uptake after zinc deprivation and seed zinc content. *Plant Molecular Biology* **54**, 373–385. doi: 10.1023/B:PLAN.0000036370.70912.34

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

Rengel Z (1999) Physiological mechanisms underlying differential nutrient efficiency of crop genotypes. In 'Mineral nutrition of crops: fundamental mechanisms and implications'. (Ed. Z Rengel) pp. 227–265. (Haworth Press, Inc.: New York)

Rengel Z (2001) Genotypic differences in micronutrient use efficiency in crops. *Communications in Soil Science and Plant Analysis* **32**, 1163–1186. doi: 10.1081/CSS-100104107

Rengel Z (2002) Genetic control of root exudation. *Plant and Soil* **245**, 59–70. doi: 10.1023/A:1020646011229

Robinson D (2005) Integrated root responses to variations in nutrient supply. In 'Nutrient acquisition by plants. An ecological perspective'. (Ed. H BassiriRad) pp. 43–62. (Springer-Verlag: Berlin)

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. *Annals of Botany* **88**, 929–940. doi: 10.1006/anbo.2001.1530

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

Runge GF, Senauer B, Pardey P, Rosengrant M (2003) 'Ending hunger in our lifetime: food security and globalization.' (Johns Hopkins University Press: Baltimore, MD, USA)

Ryan MH, Graham JH (2002) Is there a role for arbuscular mycorrhizal fungi in production agriculture? *Plant and Soil* **244**, 263–271. doi: 10.1023/A:1020207631893

Ryan PR, Delhaize E, Jones DL (2001) Function and mechanism of organic anion exudation from plant roots. *Annual Review of Plant Physiology and Plant Molecular Biology* **52**, 527–560. doi: 10.1146/annurev.arplant.52.1.527

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 and Soil* **170**, 251–265. doi: 10.1007/BF00010478

Sanchez PA (1976) 'Properties and management of soils in the tropics.' (John Wiley: New York)

Sanchez PA (2002) Ecology—Soil fertility and hunger in Africa. *Science* **295**, 2019–2020. doi: 10.1126/science.1065256

Sanchez PA, Swaminathan MS (2005) Hunger in Africa: the link between unhealthy people and unhealthy soils. *Lancet* **365**, 442–444.

Senior M, Chin E, Lee M, Smith J, Stuber C (1996) Simple sequence repeat markers developed from maize sequences found in GenBank database: map construction. *Crop Science* **36**, 1676–1683.

Setter TL, Waters I (2003) Review of prospects for germplasm improvement for waterlogging tolerance in wheat, barley and oats. *Plant and Soil* **253**, 1–34. doi: 10.1023/A:1024573305997

Shiva V (1991) The green revolution in the Punjab. *The Ecologist* **21**, 57–60.

Singh SP, Urrea CA, Gutiérrez JA, Garcia J (1989) Selection for yield at two fertilizer levels in small-seeded common bean. *Canadian Journal of Plant Science* **69**, 1011–1017.

Smith SE, Read DJ (1997) 'Mycorrhizal symbiosis.' (Academic Press: San Diego, CA)

Sprent JI (2005) Biological nitrogen fixation associated with angiosperms in terrestrial systems. In 'Nutrient acquisition by plants: an ecological perspective'. (Ed. H BassiriRad) pp. 89–116. (Springer-Verlag: Berlin)

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

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 Physiology* **127**, 1836–1844. doi: 10.1104/pp.127.4.1836

Tollenaar M, Lee EA (2002) Yield potential, yield stability and stress tolerance in maize. *Field Crops Research* **75**, 161–169. doi: 10.1016/S0378-4290(02)00024-2

Tomscha J, Trull M, Deikman J, Lynch JP, Guiltinan M (2004) Phosphatase under-producing mutants have altered phosphorus relations. *Plant Physiology* **135**, 334–345. doi: 10.1104/pp.103.036459

Tripathi SC, Sayre KD, Kaul JN, Narang RS (2004) Lodging behaviour and yield potential of spring wheat (*Triticum aestivum* L.): effects of ethephon and genotypes. *Field Crops Research* **87**, 207–220. doi: 10.1016/j.fcr.2003.11.003

Tuberosa R, Salvi S, Sanguineti MC, Landi P, Maccaferri M, Conti S (2002) Mapping QTLs regulating morpho-physiological traits and yield: case studies, shortcomings and perspectives in drought-stressed maize. *Annals of Botany* **89**(Spec. No.), 941–963. doi: 10.1093/aob/mcf134

USDA Soil Taxonomy (1999) 'Soil taxonomy: a basic system of soil classification for making and interpreting soil surveys.' 2nd edn. Agricultural Handbook No. 436. Soil Survey Staff. United States Department of Agriculture, National Resources Conservation Service.

Vance CP (2001) Symbiotic nitrogen fixation and phosphorus acquisition. Plant nutrition in a world of declining renewable resources. *Plant Physiology* **127**, 390–397. doi: 10.1104/pp.127.2.390

Vance CP (2002) Root–bacteria interactions: symbiotic N$_2$ fixation. In 'Plant roots: the hidden half'. (Eds Y Waisel, A Eshel, U Kafkafi) pp. 839–868. (Marcel Dekker, Inc.: New York)

Vance CP, Graham PH, Allan DL (2000) Biological nitrogen fixation: phosphorus a critical future need? In 'Nitrogen fixation: from molecules to crop productivity'. (Eds FO Pederosa, M Hungria, G Yates, WE Newton) pp. 509–514. (Kluwer Academic: Dordrecht, The Netherlands)

Vance CP, Uhde-Stone C, Allan DL (2003) Phosphorus acquisition and use: critical adaptations by plants for securing a nonrenewable resource. *New Phytologist* **157**, 423–447. doi: 10.1046/j.1469-8137.2003.00695.x

Vartapetian BB, Jackson MB (1997) Plant adaptations to anaerobic stress. *Annals of Botany* **79**, 3–20. doi: 10.1006/anbo.1996.0295

Veneklaas EJ, Stevens J, Cawthray GR, Turner S, Grigg AM, Lambers H (2003) Chickpea and white lupin rhizosphere carboxylates vary with soil properties and enhance phosphorus uptake. *Plant and Soil* **248**, 187–197. doi: 10.1023/A:1022367312851

Very A-A, Sentenac H (2003) Molecular mechanisms and regulation of K + transport in higher plants. *Annual Review of Plant Biology* **54**, 575–603. doi: 10.1146/annurev.arplant.54.031902.134831

Vosti SA, Reardon T (1997) 'Sustainability, growth, and poverty alleviation: a policy and agroecological perspective.' (International Food Policy Research Institute: Washington, DC)

Walk T, Jaramillo R, Lynch JP (2006) Architectural tradeoffs between adventitious and basal roots for phosphorus acquisition. *Plant and Soil* **279**, 347–366. doi: 10.1007/s11104-005-0389-6

Welch RM, Graham RD (2004) Breeding for micronutrients in staple food crops from a human nutrition perspective. *Journal of Experimental Botany* **55**, 353–364. doi: 10.1093/jxb/erh064

White P (2000) Calcium channels in higher plants. *Biochimica et Biophysica Acta* **1465**, 171–189. doi: 10.1016/S0005-2736(00)00137-1

Whiteaker G, Gerloff GC, Gabelman WH, Lindgren D (1976) Intraspecific differences in growth of beans at stress levels of phosphorus. *Journal of the American Society for Horticultural Science* **101**, 472–475.

World Bank (2004) 'World development indicators.' (The World Bank: Washington, DC)

Xie YJ, Yu D (2003) The significance of lateral roots in phosphorus (P) acquisition of water hyacinth (*Eichhornia crassipes*). *Aquatic Botany* **75**, 311–321. doi: 10.1016/S0304-3770(03)00003-2

Yan X (2005) The roots of P-efficient soybean: theories and practices. In 'Plant nutrition for food security, human health and environmental protection'. (Ed. CJ Li) pp. 36–37. (Tsinghua University Press: Beijing)

Yan X, Beebe SE, Lynch JP (1995*a*) Genetic variation for phosphorus efficiency of common bean in contrasting soil types. II. Yield response. *Crop Science* **35**, 1094–1099.

Yan X, Lynch JP, Beebe SE (1995*b*) Genetic variation for phosphorus efficiency of common bean in contrasting soil types. I. Vegetative response. *Crop Science* **35**, 1086–1093.

Yan XL, Lynch JP, Beebe SE (1996) Utilization of phosphorus substrates by contrasting common bean genotypes. *Crop Science* **36**, 936–941.

Yan X, Liao H, Beebe S, Blair M, Lynch JP (2004) QTL mapping of root hair and acid exudation traits and their relationship to phosphorus uptake in common bean. *Plant and Soil* **265**, 17–29. doi: 10.1007/s11104-005-0693-1

Yan X, Wu P, Ling H, Xu G, Xu F, Zhang Q (2006) Plant nutriomics in China—an overview. *Annals of Botany* **98**, 473–482. doi: 10.1093/aob/mcl116

Yun SJ, Kaeppler SM (2001) Induction of maize acid phosphatase activities under phosphorus starvation. *Plant and Soil* **237**, 109–115. doi: 10.1023/A:1013329430212

Zhu J, Lynch JP (2004) The contribution of lateral rooting to phosphorus acquisition efficiency in maize (*Zea mays* L.) seedlings. *Functional Plant Biology* **31**, 949–958. doi: 10.1071/FP04046

Zhu J, Kaeppler S, Lynch JP (2005*a*) Mapping of QTL controlling root hair length in maize (*Zea mays* L.) under phosphorus deficiency. *Plant and Soil* **270**, 299–310. doi: 10.1007/s11104-004-1697-y

Zhu J, Kaeppler S, Lynch JP (2005*b*) Mapping of QTL for lateral root branching and length in maize (*Zea mays* L.) under differential phosphorus supply. *Theoretical and Applied Genetics* **111**, 688–695. doi: 10.1007/s00122-005-2051-3

Zhu J, Kaeppler S, Lynch JP (2005*c*) Topsoil foraging and phosphorus acquisition efficiency in maize (*Zea mays* L.). *Functional Plant Biology* **32**, 749–762. doi: 10.1071/FP05005

Zhu J, Mickelson S, Kaeppler S, Lynch JP (2006) Detection of quantitative trait loci for seminal root traits in maize (*Zea mays* L.) seedlings grown under differential phosphorus levels. *Theoretical and Applied Genetics* **113**, 1–10. doi: 10.1007/s00122-006-0260-z