Plant Soil (2011) 349:121–156
DOI 10.1007/s11104-011-0950-4

REGULAR ARTICLE

Plant and microbial strategies to improve the phosphorus efficiency of agriculture

Alan E. Richardson · Jonathan P. Lynch · Peter R. Ryan · Emmanuel Delhaize · F. Andrew Smith · Sally E. Smith · Paul R. Harvey · Megan H. Ryan · Erik J. Veneklaas · Hans Lambers · Astrid Oberson · Richard A. Culvenor · Richard J. Simpson

Received: 1 March 2011 / Accepted: 9 August 2011 / Published online: 3 September 2011

Abstract
Background Agricultural production is often limited by low phosphorus (P) availability. In developing countries, which have limited access to P fertiliser, there is a need to develop plants that are more efficient at low soil P. In fertilised and intensive systems, P-efficient plants are required to minimise inefficient use of P-inputs and to reduce potential for loss of P to the environment.
Scope Three strategies by which plants and micro-organisms may improve P-use efficiency are outlined: (i) Root-foraging strategies that improve P acquisition by lowering the critical P requirement of plant growth and allowing agriculture to operate at lower levels of soil P; (ii) P-mining strategies to enhance the desorption, solubilisation or mineralisation of P from sparingly-available sources in soil using root exudates (organic anions, phosphatases), and (iii) improving internal P-utilisation efficiency through the use of plants that yield more per unit of P uptake.

Responsible Editor: Matthias Wissuwa.

A. E. Richardson (✉) · R. A. Culvenor · R. J. Simpson
CSIRO Sustainable Agriculture National Research Flagship/CSIRO Plant Industry,
GPO Box 1600, Canberra, ACT 2601, Australia
e-mail: alan.richardson@csiro.au

J. P. Lynch
Department of Horticulture,
The Pennsylvania State University,
University Park, PA 16802, USA

P. R. Ryan · E. Delhaize
CSIRO Plant Industry,
GPO Box 1600, Canberra, ACT 2601, Australia

F. A. Smith · S. E. Smith
Soils Group, School of Agriculture, Food and Wine,
The University of Adelaide,
Waite Campus DX 650 636,
Adelaide 5005, Australia

P. R. Harvey
CSIRO Sustainable Agriculture National Research Flagship/CSIRO Ecosystem Sciences, PMB 2,
Glen Osmond, SA 5064, Australia

A. E. Richardson · M. H. Ryan · E. J. Veneklaas · H. Lambers · R. J. Simpson
School of Plant Biology, Faculty of Natural and Agricultural Sciences, and Institute of Agriculture,
The University of Western Australia,
35 Stirling Highway,
Crawley, WA 6009, Australia

A. Oberson
Group of Plant Nutrition, Research Station Eschikon,
ETH Zurich, Institute of Agricultural Sciences,
Lindau, Switzerland

Conclusions We critically review evidence that more P-efficient plants can be developed by modifying root growth and architecture, through manipulation of root exudates or by managing plant-microbial associations such as arbuscular mycorrhizal fungi and microbial inoculants. Opportunities to develop P-efficient plants through breeding or genetic modification are described and issues that may limit success including potential trade-offs and trait interactions are discussed. Whilst demonstrable progress has been made by selecting plants for root morphological traits, the potential for manipulating root physiological traits or selecting plants for low internal P concentration has yet to be realised.

Keywords Carboxylate · Inoculant · Mineralisation · Mycorrhizas · Organic anion · Phosphatase · Rhizosphere · Roots · Solubilisation

Introduction

Low phosphorus (P) availability limits plant growth on many soils across the world and is a common constraint to agricultural productivity, particularly in developing countries where access to P fertilisers is restricted (Lynch 2007). P fertilisers, derived predominantly from rock phosphate, are used in intensive agricultural systems to overcome soil P deficiency and thus make a significant contribution to current global food production and security. However, rock phosphate reserves are a finite, non renewable resource and there is renewed concern for more sustainable and equitable use of P resources in agriculture and need to improve the efficiency with which P fertilisers are used in different agricultural systems (Bouwman et al. 2009; Cordell et al. 2009; Van Kauwenbergh 2010).

Where fertilisers are used, ideal P-balance efficiency (i.e. defined as P_{output} over P_{input} ×100; Weaver and Wong 2011) occurs when P fertiliser inputs are approximately equal to P export in products (Helyar 1998; Syers et al. 2008). However, high P-balance efficiency is often only achieved in low input, low production farming systems (e.g. McIvor et al. 2011; Burkitt et al. 2007), or in productive agriculture on soils that have intrinsically low P-buffering capacity (e.g. sands), or where P-buffering capacity is low because sorption sites for P are close to saturation and soil P fertility is relatively high (e.g. Syers et al. 2008). Elsewhere P-balance efficiency can be relatively low which contributes to an inefficient use of P. For example, in the intensive agricultural zone of southern Australia, low efficiency of P-use is illustrated by a P-balance efficiency of about 20% for grazing systems and 50% for cropping systems (McLaughlin et al. 1992; Weaver and Wong 2011). There is a number of agronomic strategies that can contribute to more efficient use of P fertilisers on farms (McLaughlin et al. 2011; Simpson et al. 2011). Plants that are more productive in soils with low plant available P concentrations, either as a result of improved foraging for P in soil or by extracting P from sparingly-available sources, also have an important role to play as their use can reduce the accumulations of P that occur in moderate to high P-sorbing soils. In fertilised agricultural systems, accumulation of P in sparingly-available inorganic and organic P pools is a major contributor to the inefficient use of P for soils that have moderate to high P-sorption capacity, whereas in soils with low P retention, losses due to P leaching can contribute to inefficient P-use (Simpson et al. 2011).

In many developing countries, P fertiliser application is low because it is a relatively expensive input (World Bank 2004), and there is a clear need to develop farming systems that can produce more with limited P availability (Lynch 2007). Productive, P-efficient plants are not in themselves a sustainable solution to these problems and they will not negate the ultimate need for P fertiliser inputs and/or recycling of P from waste streams to replace P exports (Sánchez 2010). However, more P-efficient plants provide opportunity for initial gains in crop productivity to be achieved that may subsequently assist access to fertiliser (Lynch 2007) and will also address the inefficiencies in P-balance that commonly occur where P fertilisers are used (Weaver and Wong 2011; Simpson et al. 2011). In this paper we review plant- and microbial-based strategies that have potential to improve the efficiency of P-use in agricultural systems.

Plant and microbial strategies

There are three potential strategies by which plants and microorganisms might be used to increase production in low P soil or to reduce the amount of

P fertiliser needed to maximise production (as summarised in Fig. 1):

(i) 'Root foraging strategies' that improve acquisition of soil P, support higher yields in low P soil and thus lower the critical P requirement for plant growth. This enables fertilised agriculture to be operated at lower plant available P concentrations and this, in turn, can slow the rate at which P accumulates in moderate to high P-sorbing soils (Simpson et al. 2011).

(ii) Soil P 'mining strategies' that enhance the desorption, solubilisation or mineralisation of P from sparingly-available pools (e.g. Lambers et al. 2008; 2010) and slowly mineralising or resistant organic P pools in soil (Richardson et al. 2005). Mining P from agricultural soils is not, in itself, sustainable. However, the objective of this strategy is to increase the turnover of P in sparingly-available P pools and thus to also slow the net accumulation of P that occurs when moderate to high P-sorbing soils are fertilised.

(iii) Plants with improved 'internal P-utilisation efficiency' (i.e. more plant yield per unit of P uptake) could directly reduce the amount of P fertiliser required for agricultural production. Internal P efficiency is employed to extreme levels in slow-growing species adapted to low P landscapes (Lambers et al. 2010), but is also found in some of the plant species used in agriculture (e.g. Hill et al. 2005).

In agricultural systems where it is desirable to maintain soil P fertility, the 'foraging' and 'mining' strategies can help to reduce the amount of P that must be applied to sustain production by limiting the accumulation of P in soil (Simpson et al. 2011). However, when these avenues for improving efficiency are exhausted, or when the P-balance efficiency (i.e. P exported in products as a proportion of P inputs to the soil) of an agricultural system approaches unity (i.e. 100%), reductions in the amount of P needed to sustain agriculture achieved by yielding more per unit of P uptake, or by lowering the P concentration of the products exported from a farm, are the only avenues for P-efficiency improvement.

Plants employing any of the above strategies are expected to utilise fertiliser and soil P relatively efficiently, irrespective of whether soil P fertility is being increased or maintained by P fertiliser applica-

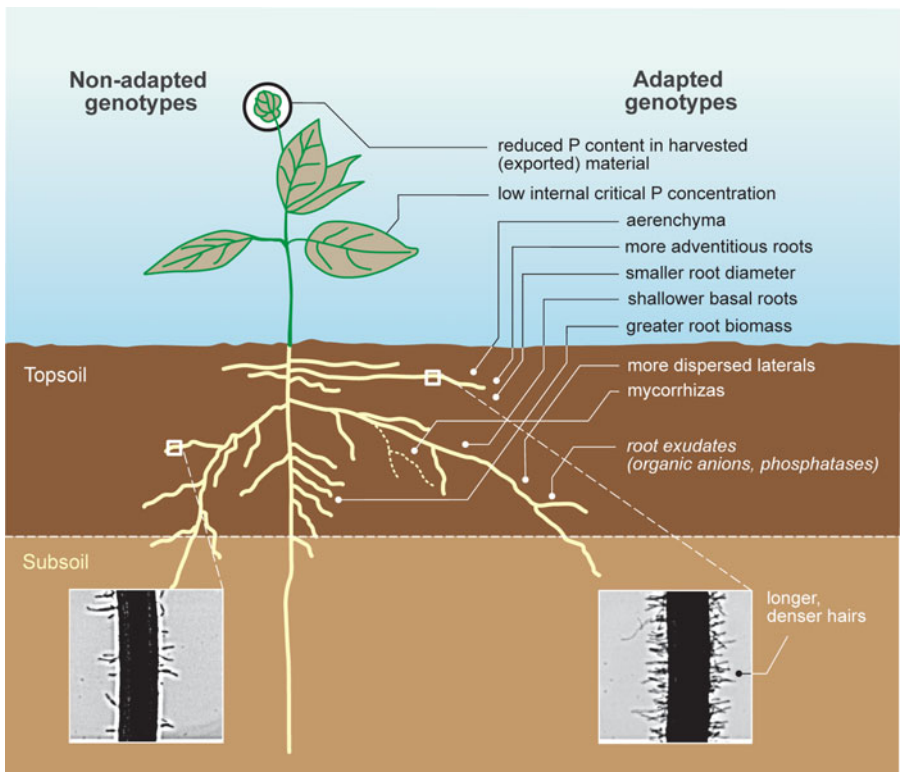


Fig. 1 Schematic representation of root and shoot phenotypes that are associated with adaptation of plants to low soil phosphorus (modified from Lynch 2007)

tions (Simpson et al. 2011), and will also yield relatively well in low P farming systems (Lynch 2007; Horst et al. 2001). The strategies are potentially independent and may provide additive benefits if co-existing in a single plant, but as discussed in this review there is also potential for trait interactions and tradeoffs.

Foraging for phosphorus through altered root morphology and architecture

Topsoil foraging

Availability of P for plants and microorganisms is typically greatest in the topsoil, so root traits that enhance topsoil foraging enhance P acquisition (Lynch and Brown 2001). Substantial differences exist for topsoil foraging within and among plant species. Root architectural traits associated with enhanced topsoil foraging include shallower growth angles of axial roots, enhanced adventitious rooting, and greater dispersion of lateral roots (Fig. 1; Lynch 2007).

In maize (*Zea mays* L.), bean (*Phaseolus vulgaris* L.), and soybean (*Glycine max* (L.) Merr) shallower growth angles of axial roots (basal roots in legumes, seminal and crown roots in maize) result in greater topsoil foraging and thereby P acquisition. Variation in root growth angle (RGA) among closely related genotypes is associated with up to 600% increase in P acquisition and 300% increase in yield in bean (Fig. 2; Bonser et al. 1996; Liao et al. 2001) and 100% increase in P acquisition in maize (Zhu et al. 2005b). Similarly in wheat (*Triticum aestivum* L.), higher root length density in upper soil layers was the most important root trait for improved P uptake in collections screened by Manske et al. (2000) and was positively correlated with P-uptake efficiency in response to application of P fertiliser. Quantitative trait loci (QTL) controlling RGA have been identified in bean, which co-segregate with yield under P stress in the field (Liao et al. 2004). Moreover, root angle can be phenotyped in young seedlings of bean or soybean under laboratory conditions, and can be phenotyped with more mature plants in the field by excavating root systems ('shovelomics'; Trachsel et al. 2011).

In bean, basal roots appear in distinct nodes or 'whorls' which influence RGA. Basal root whorl number (BRWN) varies among genotypes from one (representing four potential basal roots, since bean has a tetrach xylem anatomy) to four (corresponding to 16 potential basal roots). Topmost whorls produce shallower basal RGA, and lower whorls produce progressively steeper basal RGA, so that genotypes with greater BRWN have a greater vertical range of soil exploration, and can have 100% greater P acquisition than low BRWN genotypes (Miguel 2011). BRWN is easily phenotyped in seedlings and is under strong genetic control, with 3 QTL explaining 58% of phenotypic variance in bean (Miguel 2011). Direct phenotypic selection for RGA has been successfully used in bean breeding for low fertility soils of Africa and South America, and soybean breeding in China (Lynch 2007). BRWN is now being used as a selection criterion and as an introgression trait for bean breeding in Africa.

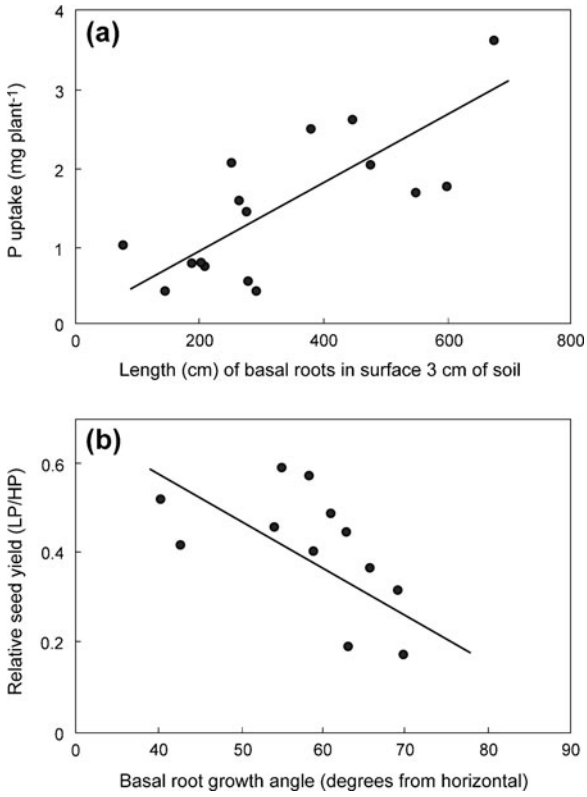


Fig. 2 Relationship between (**a**) plant phosphorus uptake and root shallowness (length of basal roots in surface soil) and (**b**) relative seed yield (expressed as yield in low P soil relative to high-P soil) and root architecture based on root growth angle for common bean (*Phaseolus vulgaris* L.) genotypes grown in low P soil (from Bonser et al. 1996 and Liao et al. 2001)

In many dicot crops, adventitious roots emerge from the subterranean portion of the hypocotyl and grow horizontally through the topsoil. Substantial genetic variation for adventitious rooting is present among bean genotypes, which was associated with growth and P acquisition in a low P soil in the tropics (Miller et al. 2003; Ochoa et al. 2006). In bean, adventitious roots have greater specific root length, lower tissue construction cost, more aerenchyma, and less lateral branching than axial roots (Miller et al. 2003). These traits are advantageous by reducing the metabolic costs of soil exploration (Lynch and Ho, 2005). *SimRoot* modelling (Lynch et al. 1997) indicates that excessive adventitious rooting may however be counterproductive for plant P acquisition by diverting resources from lateral branches of basal roots, thereby decreasing total soil exploration (Walk et al. 2006). In bean adventitious rooting appears to have complex genetic control, with 19 QTL accounting for 19 to 61% of phenotypic variation in the field (Ochoa et al. 2006). Whilst these QTL may have some application for marker assisted selection, adventitious rooting can also be phenotyped directly in the field by excavating roots.

Low P availability changes the distribution of growth among various root types. In bean and maize, growth of axial roots is maintained under low P, while initiation of lateral roots is reduced, so that lateral root density declines (Borch et al. 1999; Mollier and Pellerin 1999). The maintenance of axial root elongation could be interpreted as exploratory behaviour, allowing these roots to grow until they encounter localised patches of higher P availability, where lateral roots may proliferate (Robinson 2005). Maize genotypes with increased or sustained lateral rooting under P-deficiency had up to 100% greater P accumulation and relative growth rate than closely related genotypes with less lateral branching (Zhu and Lynch 2004). Lateral branching is under complex genetic control in maize, where 15 relatively small effect QTL have been identified (Zhu et al. 2005a). It is noteworthy that the plasticity of lateral rooting in response to P supply is itself under genetic control, indicating that plasticity is a potential selection criterion in crop breeding (Zhu et al. 2005a).

Root hairs

Root hairs are important for the acquisition of poorly mobile nutrients such as orthophosphate (Clarkson 1985; Jungk 2001; Peterson and Farquhar 1996). Several lines of evidence indicate that root hairs contribute to P acquisition, including mathematical modelling (Bouldin 1961), indirect evidence from autoradiography (Bhat and Nye 1974; Lewis and Quirk 1967), direct evidence for orthophosphate uptake by root hairs (Gahoonia and Nielsen 1998), physiological analysis of root hair mutants (Bates and Lynch 2000b; Bates and Lynch 2000c; Gahoonia and Nielsen 2003) and comparison of species and genotypes that have contrasting root hair length and density (Fig. 3; Miguel 2004; Gahoonia et al. 1999; Gahoonia and Nielsen 1997, 2004; Itoh and Barber 1983). The hyphae of arbuscular mycorrhizal (AM) fungi fulfill some of the same functions as root hairs with respect to P acquisition in plant species colonised by AM fungi (e.g. Jakobsen et al. 2005b) and have an especially large influence on P uptake in varieties with short root hairs (e.g. Schweiger et al. 1995; Miguel 2004). However, P acquisition is often improved by selecting for long root hairs (Fig. 3) even when roots are colonised by AM fungi (Miguel 2004; Wang et al. 2004; Yan et al. 2004; Zhu et al. 2010b).

Root hairs are attractive targets for crop breeding programs because there is large genotypic variation in root hair length and density, substantial effect of this variation on P acquisition, relatively simple genetic control, and opportunities for direct phenotypic selection (Gahoonia and Nielsen 2004; Lynch 2007). Genotypic variation in root hair length and density in maize and common bean is controlled by several major QTL (Yan et al. 2004; Zhu et al. 2005c), suggesting that this trait could be selected using marker assisted breeding. In addition, allocation of carbon to growth of root hairs is considered to represent a relatively minor metabolic cost to plants in order to achieve greater P efficiency (Bates and Lynch 2000a; Bates and Lynch 2000b; Ma et al. 2001a).

Reducing the metabolic costs of soil exploration

Root metabolic costs are an important component of plant growth under low P-availability (Lynch and Ho 2005). Variation for root costs is associated with P acquisition among closely related genotypes of maize and bean (Lynch and St Clair 2004; Nielsen et al. 2001; Nielsen et al. 1998; Zhu and Lynch 2004; Zhu et al. 2005b; Zhu et al. 2010a). Various root traits

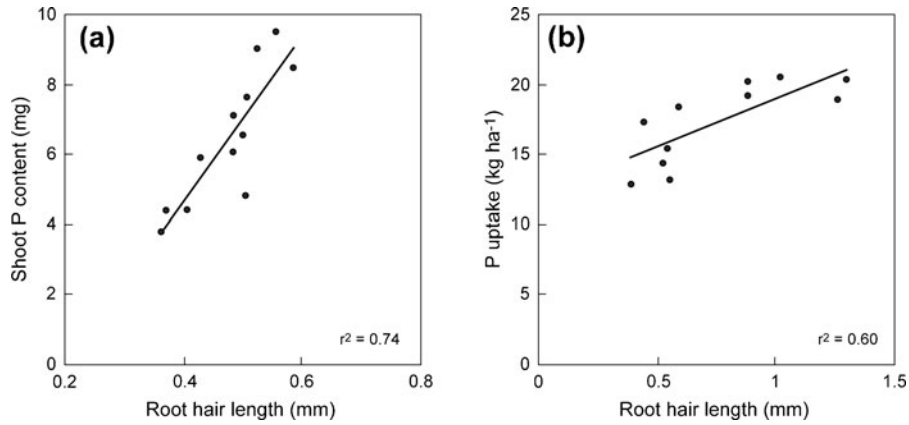


Fig. 3 a. Effect of variation in root hair length on shoot phosphorus content of common bean (*Phaseolus vulgaris* L.) genotypes. Plants were grown for 35 days in low P soil in the field in Costa Rica. Each point is the mean of 4 replicates of one genotype; the set of genotypes are six recombinant inbred lines having long or short root hairs (from Miguel 2004). **b**. Correlation between shoot P uptake and root hair length of barley (*Hordeum vulgare* L.) genotypes grown in a low P field soil (from Gahoonia and Nielsen 2004)

could alter the relationship of root growth and cost. Root architecture alters the carbon cost of soil exploration by regulating the extent of root competition within and among root systems (Ge et al. 2000; Rubio et al. 2003; Rubio et al. 2001). As indicated above, morphological traits such as root hairs enhance P acquisition at minimal carbon cost. Biomass allocation to root classes that are less metabolically demanding per unit of P acquisition, notably adventitious roots, may also reduce overall root system cost (Miller et al. 2003). Recent research indicates that anatomical traits such as root cortical aerenchyma (RCA; e.g. Fig. 4a) and delayed secondary development (root etiolation; e.g. Fig. 6a) are important for P acquisition by regulating root costs.

Although most research on RCA has focused on its importance in hypoxia, RCA can also be induced by deficiency of nitrogen (N), sulfur (S) or P (Bouranis et al. 2003; Drew et al. 1989; Fan et al. 2003; Konings and Verschuren 1980). RCA may be useful under nutrient stress by converting living cortical tissue to air space, thereby reducing the nutrient and carbon costs of root tissue while maintaining surface area for nutrient uptake (Fan et al. 2003; Lynch and Brown 1998; Zhu et al. 2010b). Genotypes of maize and bean vary in RCA formation, which in maize is strongly related to root P content and respiration, and root growth maintenance in low P soil (Fig. 4b; Fan et al. 2003). Genotypic variation in RCA formation was associated with deeper rooting, better plant water status, and 800% variation in yield under drought

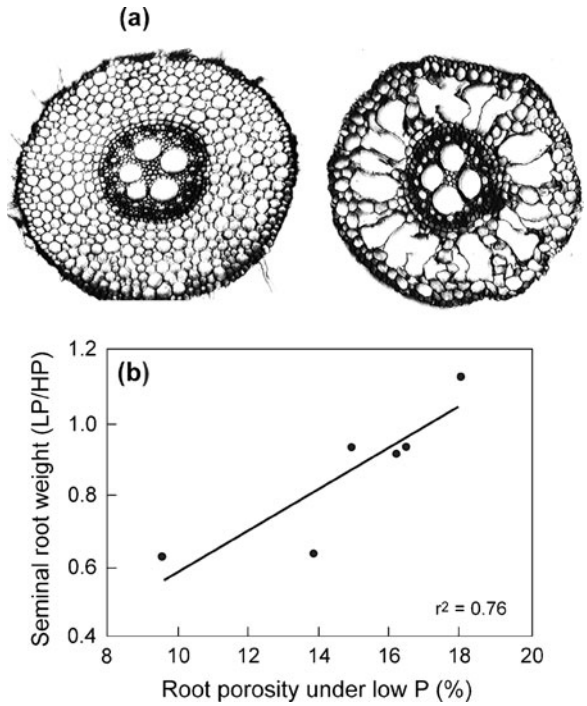


Fig. 4 a. Examples of genotypic variation in root cortical aerenchyma (RCA) formation in maize (*Zea mays* L.). **b**. Maintenance of root growth in a low P field soil as related to RCA formation in unrelated maize genotypes. Root weights of low P plants (LP) are expressed as the proportion of corresponding high-P (HP) roots and are plotted against percentage root porosity for plants grown at low P. Each point is the mean of 4 replicates (JM Zhu, SM Kaeppler and JP Lynch, unpublished)

stress in the field (Zhu et al. 2010b). *SimRoot* modelling indicates that RCA could account for up to 70% increased growth under P stress in maize and 14% in bean (Fig. 5; Postma and Lynch 2011). QTL have been identified controlling RCA formation in maize with potential application in breeding programs to enhance flooding tolerance in maize and other grains (Mano et al. 2007; Ray et al. 1999; Setter and Waters 2003).

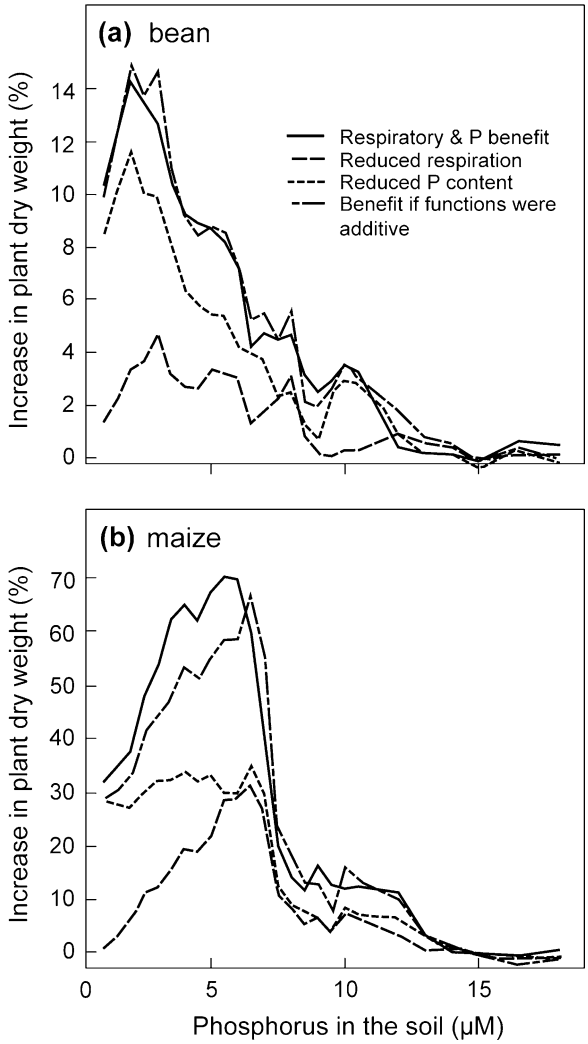


Fig. 5 Relative respiratory and phosphorus benefit on shoot growth (40 days after germination) predicted for (**a**) common bean (*Phaseolus vulgaris* L.), and (**b**) maize (*Zea mays* L.) at differing levels of soil P availability, as a result of forming root cortical aerenchyma (RCA) (from Postma and Lynch 2011). Data are from *SimRoot* simulations and relative benefit was calculated as shoot yield achieved with RCA relative to shoot yield without RCA. The sizes of the RCA were assumed to be 39.3% and 26.8% of root cross-sectional area for maize and bean, respectively (Fan et al. 2003)

Dicots have secondary root growth which results in expansion of root diameter over time. Bean roots under P stress show reduced secondary development and therefore reduced root expansion in favour of continued root elongation, a process called 'root etiolation' by analogy with shoot response to low light intensity (Fig. 6a; Eshel et al. 1995; Fan et al. 2003; Lynch 2007; Lynch and Brown 2006). Bean genotypes vary in this response which is related to root metabolic costs and soil exploration (Morrow de la Riva 2010). *SimRoot* modelling indicates that genetic variation for this trait in bean may account for a 38% increase in shoot growth over the first 40 days of growth under low P (Fig. 6b). It is possible that this trait has been subject to indirect selection in bean breeding for low P environments (Beebe et al. 2006).

Arbuscular mycorrhizal symbioses

Arbuscular mycorrhizal (AM) symbioses are widespread in the plant kingdom and contribute significantly to plant P nutrition and growth in natural ecosystems (Smith and Read 2008). AM fungi colonise most agricultural species (exceptions include *Brassica* spp., and *Lupinus* spp.) and have an important role in the P nutrition of many farming systems worldwide, especially on soils with low available P (e.g. Thompson 1987). However, advantages in increased P-uptake and growth over comparative, non-mycorrhizal plants at low P, diminish with increasing soil P availability. There is often little growth advantage at soil P levels necessary for near maximum plant growth rates in intensive agricultural systems (e.g. Thomson et al. 1986; Schweiger et al. 1995). In some instances, growth rates of AM plants are less at high soil P than those of comparative non-mycorrhizal plants (Johnson et al. 1997).

Phosphorus-uptake responses of mycorrhizal plants

Many studies in which soil P pools have been labeled (e.g. with ^{32}P or ^{33}P) provide strong evidence that AM- and non-mycorrhizal plants take up P from the same soil sources (Bolan 1991; Yao et al. 2001). However, AM fungal hyphae extend further from roots than root hairs (centimetres compared with

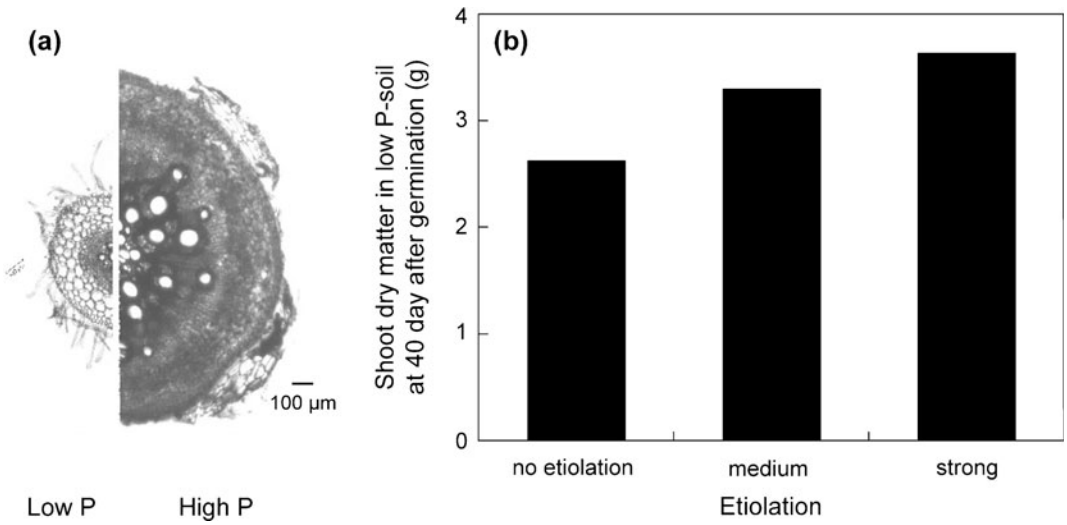


Fig. 6 **a**. Cross section of common bean (*Phaseolus vulgaris* L.) basal roots grown for 6 weeks with low (1 µM) or high (1 mM) phosphorus, showing reduced secondary growth under low P (root etiolation). Root sections shown are from equivalent positions on roots of the same age. **b**. Effect of root etiolation on bean growth for 40 days after germination under low P, as simulated in *SimRoot* (JP Lynch, unpublished)

millimetres; Smith and Read 2008), and are also active in the more mature regions of the root. Hence, the larger soil volume that can be exploited by AM plants is considered to be the reason when greater P uptake is achieved in low P soil. Advantages of AM symbiosis over the non-mycorrhizal state of the same plant genotype are inextricably associated with root architecture, in that plants with extensive, branched root systems, very fine roots and long root hairs tend to show relatively low improvement in growth when they are mycorrhizal, even in low P soils (Schweiger et al. 1995; Miguel 2004). It is clear that AM fungi play a role similar to root hairs in P acquisition and can compensate wholly or partly when root hairs are short, as shown with beans (Miguel 2004), pasture legumes (Caradus 1981; Schweiger et al. 1995), and a 'bald-root' barley (*Hordeum vulgare* L.) mutant (Jakobsen et al. 2005a). Because of the extent of external AM fungal hyphae over centimetres combined with their relatively small diameter and thus ability to effectively explore soil, it is not obvious why positive AM growth responses can be entirely lacking. Possible physiological explanations are discussed later. It may also be relevant that non-mycorrhizal controls in experiments can have higher root hair frequency and length compared with the AM plants and also increased branching (e.g. Kothari et al. 1990; Hetrick 1991).

The decline in positive AM fungal growth responses with increasing plant available soil P varies greatly among plant genotypes (e.g. Baon et al. 1993; barley cultivars; Hetrick et al. 1996; wheat cultivars) and also fungal genotypes (e.g. Thomson et al. 1986). The proportion of root length that is colonised by AM fungi also tends to decrease with increasing soil P, and this is often taken to mean that the plant is suppressing the AM symbiosis. However, total colonisation per plant may not decrease until soil P levels are very high and it is likely that the decline in percent colonization of roots that is often observed at intermediate P levels (e.g. Ryan et al. 2000) is a consequence of roots growing faster than the rate at which they can be colonised by the AM fungi (Thomson et al. 1986; Smith and Smith 2011). Although there are some clear examples where crops have grown poorly when AM fungal propagules were depleted (e.g. after long fallow periods in a subtropical wheat system, Thompson 1987, 1991), AM symbioses have a mixed reputation worldwide as a means of improving crop growth, particularly under high soil P conditions. The reason for this is the lack of obvious nutritional benefits to the crop, or a perceived 'parasitic' effect that constrains crop yield under high soil P conditions. Consequently, it has been suggested that there may be benefits to production by managing crop rotations to reduce AM fungal

colonisation or by breeding plants for less colonisation (Ryan and Graham 2002; Ryan et al. 2005). However, recent experiments using labelled-P supplied to external hyphae of AM fungi in a compartment unavailable to roots have shown that the AM-path for P uptake operates in wheat, barley and other plants with no or negative AM fungal growth responses, as it does in plants showing positive growth responses to AM colonisation (Smith et al. 2011). In such plants, the root epidermal (direct-path) for P uptake is suppressed (e.g. Li et al. 2006). A similar approach has been used to demonstrate qualitatively that the AM pathway operates in wheat in the field (Schweiger and Jakobsen 1999). The physiological measurement of the operation of the AM path for P uptake is complemented by the expression of AM-inducible phosphate transporters in roots, again irrespective of size or direction of the growth response to AM fungal colonisation (Glassop et al. 2005; Javot et al. 2007; Grace et al. 2009). Accordingly, the physiological basis for AM fungal 'parasitism' is being reassessed (Smith and Smith 2011; Smith et al. 2011).

Mycorrhizas are inevitably involved in the phosphorus nutrition of many agricultural plants

Colonisation of roots by AM fungi is the rule rather than the exception for most agricultural plants, even though levels of colonisation can vary greatly, depending on farming practice and environmental conditions. Because plant P nutrition can be improved by altering root architecture, morphology or root hair length and density, and the root system is the scaffold for AM fungal colonisation, it is expected that changes to root architecture will also alter the influence of the AM fungi that colonise the roots. Less well understood, however, is how much root architecture itself is altered by AM fungal colonisation, apart from the few cases noted above. The ubiquitous nature of colonisation of roots and the impact that this has on the path by which orthophosphate is taken up (i.e. AM- or direct-path), suggests that AM fungi are inevitably involved in the P nutrition of AM-colonised plants even when a positive growth response to colonisation cannot be demonstrated. The realisation that the symbiotic interaction can result in suppression of the direct-path (via plant root or root hairs) for P uptake may provide clues to some of the less intuitive aspects of the P nutrition of AM plants. Growth depressions associated with AM fungal colonisation are conventionally considered to be a consequence of the carbon cost of supporting the AM fungal symbiosis. However, growth depressions can occur when colonisation of roots and external hyphal length density are very low. Under these conditions the carbon cost of the AM symbiosis is expected to be low also, so the growth depressions may be associated with inhibition of the plant P-uptake pathway (Li et al. 2008).

It is presently unclear why P uptake by the plant- and AM fungal-paths are not additive, giving a positive AM growth response in every case where roots are colonised. Resolution of this dilemma requires knowledge of the molecular processes involved in the regulation of P-uptake in AM plants and may provide the insight required to harness the potential soil foraging benefits of AM fungi for plants, and in agronomic circumstances, where P-uptake benefits are not currently realised. However, disentangling the combined role of plant and AM genotypes, soil chemistry and other environmental factors remains a formidable challenge.

Enhancing the desorption or mobilisation of phosphorus from sparingly-available pools in soil

Specialist root structures and exudation of organic anions (carboxylates) by roots

In soils with extremely low available P (e.g., many Australian soils under native vegetation) clustering of rootlets with abundant root hairs is a prominent root specialisation (Lambers et al. 2010). Proteaceae and a number of phylogenetically unrelated species have proteoid (cluster) roots, while dauciform and capillaroid roots are found in Cyperaceae and Restionaceae, respectively (Lambers et al. 2006). The concentration of rootlets or root hairs in small soil volumes, rather than exploring larger soil volumes, is clearly not the optimal morphology for scavenging low concentrations of diffusely available P. Instead, the cluster root morphology is consistent with a mining strategy (Lambers et al. 2006). Species with cluster roots are particularly abundant on severely weathered soils where recycling of P from aboveground litter and belowground root turnover is virtually the only source of P, and on highly weathered and strongly P-sorbing

soils that have reasonable amounts of total P, but where it is not available to plants that do not have a specialised mechanism to mobilise the P (Lambers et al. 2006). Root clusters are positioned in soil horizons or patches that have above-average total P but low levels of plant available P (e.g. Pate et al. 2001, Lambers et al. 2011), are rich in organic matter, or occur under decomposing litter (Lamont 1973). It is widely recognised that these roots are effective for capturing P that is mobilised from sparingly-available soil P. The root clusters alter soil chemistry by release of root exudates, including organic anions (mono-, di- and tricarboxylates), enzymes, phenolic acids and protons, with organic anion exudation usually regarded as the primary factor in the mobilisation of sparingly-available P.

While cluster roots, dauciform roots and capillaroid roots are most abundant in Proteaceae, Cyperaceae and Restionaceae on severely P-impoverished soils, their presence is not limited to these phylogenetic groups nor to extremely infertile soils (Skene 1998; Lambers et al. 2011). White lupin (*Lupinus albus* L.) is an established crop species that has cluster roots indicating that the specialised root structures can be used in agricultural production systems. For example, in Chile white lupin is cultivated widely on young volcanic soils that contain large amounts of poorly available P (Huyghe 1997). However, P acquisition traits may not be expressed in all cropping situations because increasing soil P availability reduces investment in cluster roots to almost zero in all species (Reddell et al. 1997; Shane et al. 2003a; Shane et al. 2003b; Shane et al. 2006; Abdolzadeh et al. 2010). This may reduce their effectiveness when being deployed to mobilise P for use by other crops, or as part of a strategy to reduce the accumulation of sparingly-available P in fertilised soils (e.g. Simpson et al. 2011).

Considerable plasticity in cluster root investment, placement and activity has been demonstrated in native Australian legumes (Adams et al. 2002; Shane and Lambers 2005) and in white lupin (Shu et al. 2007a, b). Studies in white lupin exposed different parts of the root system to different levels of P, and showed that while overall investment in cluster roots was suppressed when more P is available, cluster roots preferentially grew in P-enriched parts of the soil, even when enriched with inorganic P. Moreover, the concentrations of organic anions were enhanced when the added P was iron (Fe) phosphate or hydroxyapatite (Shu et al. 2007a, b). Split root experiments indicate that the response of cluster roots to locally enriched-P also differs markedly between species. For example, when one side of the root system experienced higher P concentration in hydroponics, Hakea species (*Hakea prostrata* R.Br. and *H. trifurcata* (Sm.) R.Br.) produced lower cluster root mass on that side compared to the low P side. In contrast, grevillea (*Grevillea crithmifolia* R.Br.) and lupins (*Lupinus mutabilis* Sweet and *L. albus*) produced more cluster root mass on the high-P side (Shane and Lambers 2005). This adaptive deployment of the cluster roots suggests that it may be feasible to enhance P acquisition in agriculture by using cluster root species in combination with banded fertiliser placement. Concentrated banding of fertiliser allows adequate fertility for high production to be achieved, but a patchy distribution of P may also be suitable for expression of the P-mining attributes of cluster roots.

Alteration of rhizosphere chemistry is not limited to species with root clusters. In the *Lupinus* genus, species that do not form cluster roots may have similar rhizosphere pH and organic anion concentrations to those that do (Hocking and Jeffery 2004; Pearse et al. 2006). High rhizosphere concentrations of organic anions have also been reported in other grain legume crops such as pigeon pea (*Cajanus cajan* (L.) Millsp.), chickpea (*Cicer arietinum* L.) and field pea (*Pisum sativum* L.) (Ae et al. 1991; Veneklaas et al. 2003; Nuruzzaman et al. 2005; Pearse et al. 2006), as well as a range of perennial legume species (Pang et al. 2010). In many species, exudate concentrations are responsive to plant P status and are reduced at high levels of soil P fertility. In some species, exudation appears to be constitutive and sometimes at high rates, for example, the exudation of malonate in chickpea (Wouterlood et al. 2005).

There is good evidence that cluster roots enable plants to access soil P pools that are poorly-available to species that do not have this mechanism (e.g. Hocking et al. 1997). However, it is less clear if exudation of organic anions from plants that do not have the cluster root morphology also increases their access to sparingly-available P. For example, Pearse et al. (2007) found that wheat took up more P from $AlPO_4$ than three lupin species. So, even though diffuse fine root systems may not be effective in mobilising sparingly-available soil P, there will always

be small amounts of P in solution and these may be scavenged by such roots (e.g. Barrow 1980). Pearse et al. (2007) also noted that field pea and chickpea were unable to access $AlPO_4$ or $FePO_4$ in sand culture despite releasing organic anions (carboxylates) into the rhizosphere (Pearse et al. 2007). In a separate study, P uptake by chickpea from 11 different soils did however correlate with organic anion concentrations in the rhizosphere (Veneklaas et al. 2003). Organic anion exudation from roots has thus been embraced widely as a likely mechanism for improving the access to sparingly-available P by agricultural crops. Our observations of the P nutrition of species that naturally secrete organic anions indicate that that this strategy needs to be thoroughly understood if it is to deliver the promise of improved P-use efficiency in agricultural systems.

Can the release of organic anions from roots mobilise soil phosphorus?

It has been hypothesised widely that the release of organic anions from roots can improve P nutrition by mobilising sparingly-available pools of P into the soil solution. The organic anions are reported to occupy sorption sites on soil minerals that might otherwise bind P, and replace P in the sparingly-soluble complexes that form with aluminium (Al), Fe and calcium (Ca). The idea is based on many studies reporting two types of observations: (i) the release of citrate, malate and oxalate from roots of certain species increases with the onset of P deficiency, especially from those with cluster roots (Jones 1998; Vance et al. 2003; Ryan et al. 2001; Neumann and Martinoia 2002); (ii) organic anions can liberate more P into soil solution than similar treatments with water (Fig. 7; Fox et al. 1990; Gerke 1992; Jones 1998; Khademi et al. 2009; 2010) along with greater release of organic forms of soil P (Hayes et al. 2000a; Wei et al. 2010).

Organic anion exudation from roots has now been reported in many species in response to P deficiency or Al toxicity. Comparisons of organic anion release rates between species are difficult due to the range of units employed, but the highest rates appear to occur in white lupin and members of the Proteaceae (up to 3 μmol citrate g^{-1} FW h^{-1}; Roelofs et al. 2001). However, despite extensive literature implicating root exudates in P mobilisation, the evidence that organic anion release can improve P nutrition (particularly for species that do not form cluster roots) is modest. Many studies fail to consider whether the magnitude of organic anion efflux is sufficient to influence P availability and it is often forgotten that other plant responses occurring in parallel may have contributed to nutrient efficiency. Even the seminal studies on white lupin (Gardner et al. 1981; Gardner et al. 1983) only provide indirect evidence because (as discussed above) citrate efflux cannot be separated from the formation of cluster roots and the release of other exudates (phosphatases, protons, secondary metabolites) which may also contribute to improved P nutrition. Other evidence that supports a beneficial role for organic anions include in vitro studies that demonstrate, albeit highly dependent on soil type, that local injections of citrate and oxalate into the rhizosphere can mobilise P and increase its uptake by plants (Ström et al. 2002; Khademi et al. 2010) and evidence that organic anions can increase the diffusion coefficient of orthophosphate in the soil solution by two or three orders of magnitude (Gerke 1994). Modelling supports a role for organic anions in mobilising P bound by metal ions (Kirk 1999).

Soluble organic anion concentrations measured in a range of soil types are generally less than 50 μM, with concentrations in the rhizosphere usually greater than those in bulk soil. Values of 5 to 50 μmol citrate g^{-1} soil (cluster roots of white lupin; Dinkelaker et al. 1989; Gerke 1992) likely correspond to soluble citrate concentrations of 1 to 10 mM in soil solution and are consistent with measurements using ceramic suction cups (Dessureault-Rompre et al. 2007). These concentrations are substantial and likely to benefit plant nutrition, because in vitro studies estimate that 1 mM citrate or oxalate can be effective for mobilisation of P in some soils (Fig. 7; Gerke 1994; Kirk 1999; Jones et al. 2003; Khademi et al. 2010). However, further work is needed to establish the relationship between localised concentrations of organic anions in a rhizosphere and the amount of P that can be released for plant uptake in different soils.

Attempts have been made to address the uncertainties discussed above by modelling and/or attempting to determine empirically how much orthophosphate can be mobilised by the organic anion concentrations measured in rhizospheres. However, this is a challenging task. It is particularly difficult to sample at the scale required because organic anions released from roots are unlikely

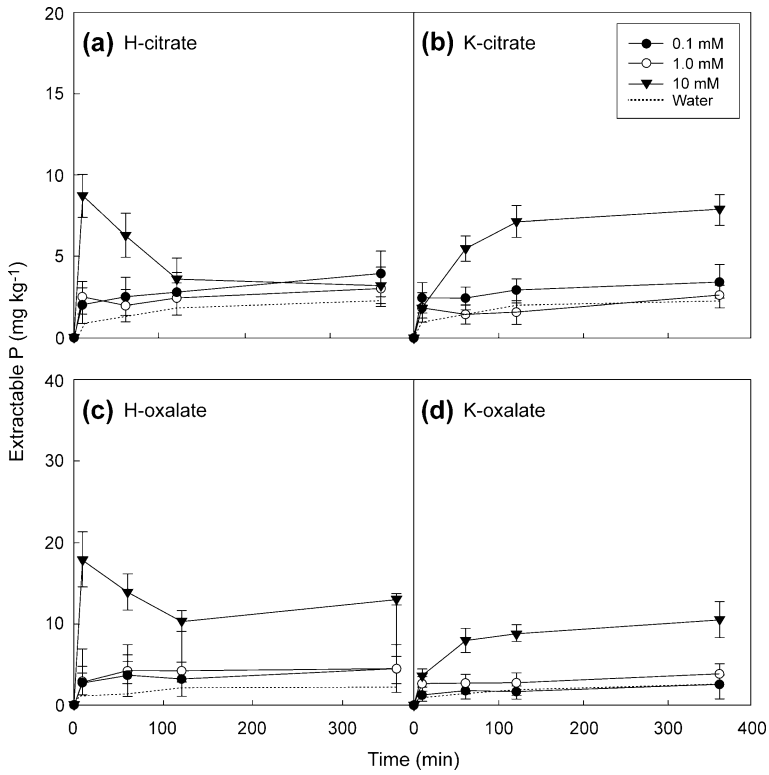


Fig. 7 Phosphorus extracted from soil by water (*dotted line*) and two organic anions at differing concentrations from 3 calcareous soils (values are the mean of the three soils± standard error, n=3). Extractions were conducted using organic acids, as (**a**) H-citrate and (**c**) H-oxalate, or as organic anions at neutral pH as (**b**) K-citrate (potassium citrate) and (**d**) K-oxalate (potassium oxalate). Data is from Khademi et al. (2009)

to diffuse farther than a few millimetres, with most remaining close to the root surface. An exception is white lupin where the high exudation increases organic anion concentrations to beyond 6 mm distance from cluster roots (Dessureault-Rompre et al. 2007). Even careful measurement of soil adhering closely to roots may underestimate by orders of magnitude the local concentrations of organic anions in water filled spaces near the root surface (Jones et al. 2003). Uncertainties with soil chemistry including lack of information about the rates with which orthophosphate and organic anions are removed and replaced in soil solution make predictions of organic anion effects difficult. For example, Oburger et al. (2011) reported complementary effects of co-acidification on the effectiveness of different organic anions for mobilisation of P in different soils with the relative effectiveness of acidification on either ligand promoted mineral dissolution (chelation capacity) or direct ligand exchange (sorption reactions) being highly dependent on soil type. Such effects are likely to be further complicated by spatial heterogeneity within the rhizosphere (including soil mineralogy, localised soil chemistry and water content) and the unpredictable effects of microorganisms on organic anion concentrations, through their capacity to either degrade organic anions or as a potential alternative source of anions. The rhizosphere generally supports a large microbial biomass because root exudates, including organic anions, represent a readily-available carbon source. It is notable that white lupin releases several compounds that are thought to inhibit the microbial degradation of organic anions (Weisskopf et al. 2006). In vitro estimates of the half-lives of organic anions vary from less than 0.5 h for malate in a Cambisol to more than 24 h for oxalate in a Podsol (Jones and Darrah 1994; Kirk 1999; Oburger et al. 2009). A further complication for these studies, and those addressing the efficacy of organic anion release, is that in soils with high sorption capacity anions can be bound to mineral surfaces where they are less likely to be degraded by microorganisms (Oburger et al. 2009).

The ion fluxes that balance anion release from the root cells are also important, because they can influence the effectiveness of the ligand exchange reactions. The sustained efflux of organic anions from root cells cannot occur without an equal efflux of cations or an influx of anions to satisfy electro-neutrality. Citrate and malate efflux from white lupin

is partly balanced by H^+ efflux because the rhizosphere around cluster roots becomes significantly more acidic than the bulk soil (Dinkelaker et al. 1995; Yan et al. 2002; Sas et al. 2001). Although localised regions of low pH might assist in mobilising P, especially in alkaline soils, organic anions are unlikely to be as effective in very acidic environments because a greater proportion will carry smaller net charge. For instance, the pKa's of malic acid are 3.4 and 5.1, which means that at pH 3.4 approximately half of the malate is present as malic acid and half as H:malate^{1-}. Neither of these species will bind with Fe, Al or Ca ions as effectively as the divalent anion malate^{2-} which is more prevalent at higher pH. However acidification would suit the activity of acid phosphatases also released from these cluster roots (Zinn et al. 2009) and perhaps slow down the degradation of organic anions by microorganisms (see below: Khademi et al. 2010). In contrast, the exudation of a large range of organic anions from cluster roots of several members of the Proteaceae is not associated with acidification (Roelofs et al. 2001). Even in white lupin there is evidence that K^+, Na^+ and even Mg^{2+} efflux are more important than protons in maintaining electroneutrality (Zhu et al. 2005d). Malate efflux from Al-resistant wheat roots is also accompanied by K^+ and not H^+ efflux (Ryan et al. 1995). In fact, the pH around wheat root apices increases (Wherrett et al. 2005) which would be expected as malate equilibrates in the apoplasm and a proportion of the divalent anions bind with protons to become monovalent anions.

Genetic approaches likely provide an alternative opportunity for quantifying the influence of organic anions on plant nutrition. Importantly the development of germplasm with more uniform genetic background allows the contribution of traits of interest to be assessed independently from other traits that may also contribute to the phenotype. Generation of such populations, such as recombinant inbred lines, doubled haploid lines or F_3 families can be used to identify QTL which are genetically linked to root traits and for the subsequent development of breeding lines. Whilst QTL have helped link root morphology with P nutrition (e.g. Lynch 2007; Lynch and Brown 2008), no studies have demonstrated the same benefit of organic anion release apart from indirectly enhancing Al (Al^{3+}) resistance (Delhaize et al. 2009).

Genetic manipulation of plants for enhanced exudation of organic anions

Attempts to genetically manipulate plants for enhanced exudation of organic anions from roots can be broadly divided into strategies that aim to alter biosynthesis and those that focus on transport processes. For an organic anion to be secreted by roots, a biosynthetic pathway with the capacity to generate and maintain sufficient amounts during periods of peak efflux is required. However, the organic anions considered to be effective in mobilising mineral P (e.g. citrate, malate and oxalate) exist as anions in the cytosol and do not readily move unassisted across the plasma membrane to the external medium. Transport of these organic anions is facilitated by specific transport proteins embedded in the membrane, and in many cases it is the transport of organic anions and not their biosynthesis that appears to be the rate limiting step for their secretion (Ryan et al. 2001; Ryan and Delhaize 2010). In the absence of cloned genes for transport proteins the earliest attempts at enhancing organic anion efflux focused on biosynthetic pathways for which many of the genes were readily available for genetic manipulation.

The most spectacular success with the approach of modifying organic anion biosynthesis came from tobacco (*Nicotiana tabacum* L.) genetically modified to express a bacterial gene for citrate synthase. Originally designed to enhance citrate secretion as a means of conferring Al^{3+} resistance on acid soils (de la Fuente et al. 1997), the same plants modified to express a citrate synthase gene from *Pseudomonas aeruginosa* showed enhanced ability to mobilise P from an alkaline soil and, under restricted P nutrition, yielded more seed than a control (López-Bucio et al. 2000). Reports showing that over-expression of citrate synthase of mitochondrial origin in *Arabidopsis thaliana* (L.) Heynh. and carrot (*Daucus carota* L.) cell cultures produced similar phenotypes, although somewhat attenuated, appeared to support the notion that enhancing the biosynthesis of organic anions could increase their efflux from roots to enhance P nutrition (Koyama et al. 1999; Koyama et al. 2000).

Subsequent attempts to repeat the findings with the citrate synthase gene from *P. aeruginosa* or a mitochondrial citrate synthase gene from tobacco were unsuccessful (Delhaize et al. 2001; Delhaize et al. 2003). Despite generating tobacco plants with

100-fold more citrate synthase protein than the original report by de la Fuente et al. (1997), as well as using the genetic material from that study, in neither case was enhanced citrate efflux detected in the transgenic plants (Delhaize et al. 2001). These findings indicate that genetically engineering of plants with citrate synthase genes is presently not a reliable and robust strategy for enhancing organic anion efflux. In another study that focused on Al^{3+} resistance, Anoop et al. (2003) showed that rapeseed (canola; *Brassica napus* L.) that over-expressed a mitochondrial citrate synthase gene from *A. thaliana* showed enhanced citrate efflux. However, although citrate efflux was doubled in the absence of Al^{3+}, it is unlikely that these relatively small fluxes would have been very effective to enhance P nutrition.

With the reports of success in genetically modifying plants for organic anion biosynthesis with the citrate synthase genes, attention was also directed towards other key enzymes involved in organic acid biosynthesis. Overexpression of malate dehydrogenase but not phosphoenolpyruvate carboxylase (PEPC) resulted in enhanced efflux of a range of organic anions from roots of lucerne (alfalfa; *Medicago sativa* L.), and the enhanced P nutrition of the transgenic plants when grown on acid soil was attributed to the greater efflux of organic anions (Tesfaye et al. 2001). However, this conclusion is questionable given that the transgenics were reported to have increased Al^{3+} resistance and the improved acquisition of P is more likely to have been indirect due to more vigorous root growth of the transgenics in the acid soil rather than a direct effect of the organic anions solubilising mineral forms of P. In contrast to lucerne, overexpression of PEPC in rice (*Oryza sativa* L.) enhanced oxalate efflux from roots but the effect that this may have had on the P nutrition of plants grown in soil was not assessed (Begum et al. 2005).

The cloning of genes encoding proteins that transport organic anions provide an alternative means of enhancing exudation. These proteins belong to two distinct families of membrane proteins the MATE and ALMT families (Delhaize et al. 2007). Initially all the cloned genes encoded transport proteins that required Al^{3+} to activate organic anion efflux and all were involved in Al^{3+} resistance mechanisms. For instance, barley genetically modified with the *TaALMT1* gene from wheat showed at least a 20-fold greater Al^{3+}-activated malate efflux than controls and this conferred greatly increased Al^{3+} resistance (Sasaki et al. 2004; Delhaize et al. 2004). When grown on an acid soil, the transgenic barley had improved P nutrition, but this could be largely attributed to improved root growth allowing better exploration of the soil (Delhaize et al. 2009). Subsequently, genes encoding members of both the MATE and ALMT families were cloned that transported organic anions in the absence of Al^{3+} activation. These proteins have diverse roles and function in stomata (Sasaki et al. 2010; Gruber et al. 2010), vascular tissues (Durrett et al. 2007; Yokosho et al. 2009) and in maintaining malate homeostasis within cells (Kovermann et al. 2007). When ectopically over-expressed, AtFRD3 from *Arabidopsis* (Durrett et al. 2007) and HvALMT1 from barley (Gruber et al. 2011) confer organic anion efflux that is independent of Al^{3+}. In both cases the enhanced organic anion efflux conferred increased Al^{3+} resistance but any effects on P nutrition were either not assessed (Durrett et al. 2007) or confounded by a severely stunted phenotype (Gruber et al. 2011).

In summary, although there is evidence that altering organic anion biosynthesis can change internal concentrations of the major organic anions, the resulting effects on efflux appear small. These relatively small effects on efflux (2- to 4-fold) can enhance Al^{3+} resistance, but in most cases this functions on top of an existing endogenous transport mechanism for organic anions that is activated or induced by Al^{3+}. In many species, Al^{3+} increases the efflux of organic anions by a factor of ten or more, and there are few reports of similar transport mechanisms being induced under P deficiency (Ryan et al. 2001; Kochian et al. 2004). For example, even for the most optimistic case above where tobacco was engineered with a bacterial citrate synthase gene, the efflux in the absence of Al^{3+}, such as on an alkaline soil, would be negligible and enhancing the efflux by only 4-fold was unlikely to have provided sufficient organic anions to improve P nutrition. Any benefit to P nutrition on acid soil is difficult to attribute to organic acids acting directly on mineral forms of P and is more likely to be due to enhanced root growth due to improved Al^{3+} resistance. To date, unequivocal evidence of improved P nutrition has not been demonstrated from transgenic plants with enhanced organic anion exudation using appropriate controls and methods that show the acquisition of P forms not

readily available to the controls (such as L-values). The recent cloning of genes encoding transport proteins provides the tools for a strategy with greater likelihood of success for increasing organic anion efflux to levels that could benefit P nutrition. Although most of these transport proteins are Al^{3+}-activated, they provide 'in principle' evidence that efflux from roots can be substantially increased. The more recent cloning of genes encoding transport proteins that do not require Al^{3+} for activation (e.g. Durrett et al. 2007) provide an avenue for enhancing organic anion transport on a wider range of soil types. To date these proteins function in the transport of organic anions within specific plant tissues and whether they can be engineered to enhance efflux of organic anions from roots to levels required for improved P nutrition remains to be established. To achieve exudation of organic anions to levels approximating those found in white lupin may require that both transport and biosynthetic capacity be engineered in concert. Although yet to be demonstrated, the necessary tools are becoming available and it is feasible that this aim might be achieved.

Phosphatases and utilisation of soil organic phosphorus by plants

Organic forms of P in soil constitute a significant component of total soil P and contribute substantially to the overall operation of the soil P cycle. Cycling of P through organic pools is not only important in natural ecosystems (Polglase et al. 1992) and lowly fertilised grasslands, where there is significant return of plant- or animal-based residues, but also in farming systems with high dependence on external P inputs that may either be organic (e.g. manure-based systems) or reliant on inorganic fertilisers (Oberson et al. 1996; Magid et al. 1996; Simpson et al. 2011). Substantial flows of P occur between inorganic and organic pools of soil P through immobilisation and mineralisation; processes that are mediated largely by the activity of soil microorganisms (Richardson 1994; Oberson and Joner 2005; Richardson and Simpson 2011; Richardson et al., 2009a). Mineralisation of organic P (i.e. hydrolysis of organic P substrates to release orthophosphate) is essential, because orthophosphate anions (primarily as $H_2PO_4^-$ or HPO_4^{2-}) are transported across the root plasmalemma. There is little evidence to support direct uptake of organic P substrates by plants, although uptake followed by hydrolysis within the apoplast or at the root endodermis is likely (Richardson et al. 2005).

Enhancing the utilisation of organic phosphorus in soil

From a P-use efficiency perspective, the challenge is to increase the utilisation of organic P for plant production, either as a consequence of modified agronomic practices (Simpson et al. 2011) or by using plants or microorganisms capable of enhancing the mineralisation of organic P (Richardson et al. 2009a, b). Increased utilisation of organic P may occur either as a result of enhancing the overall rate of P cycling through organic matter pools (i.e. from organic matter or soil humus fractions) which can be achieved, for example, through green manure management (Simpson et al. 2011; Fageria 2007; Cherr et al. 2006; Condron 2004), or by enhancing the mineralisation of specific forms of organic P that are poorly available to plants and/or microorganisms and consequently accumulate in soil.

Mineralisation of organic P occurs through the activity of phosphatase enzymes. Soils have demonstrable phosphatase activity and substantial increases in activity have been shown to occur in the rhizosphere of plants, with many studies showing this to be associated with a depletion of soil organic P (Asmar et al. 1995; Gahoonia and Nielsen 1992; Chen et al. 2002; George et al. 2002b; Tarafdar and Jungk 1987). In vitro assays with excess concentrations of different phosphatase enzymes also indicate that, depending on soil type and previous fertiliser history, significant amounts of orthophosphate can be released from organic P in soil extracts and soil suspensions (Fig. 8; George et al. 2007a, b; Bünemann 2008). In pot experiments, plants are able to effectively utilise P from a wide range of organic sources through mineralisation by phosphatases of either plant or microbial origin (Adams and Pate 1992)

Phosphatase activity of plant roots and the potential for accessing soil organic phosphorus

Extracellular phosphatase activities of plant roots vary considerably between and within species for a wide

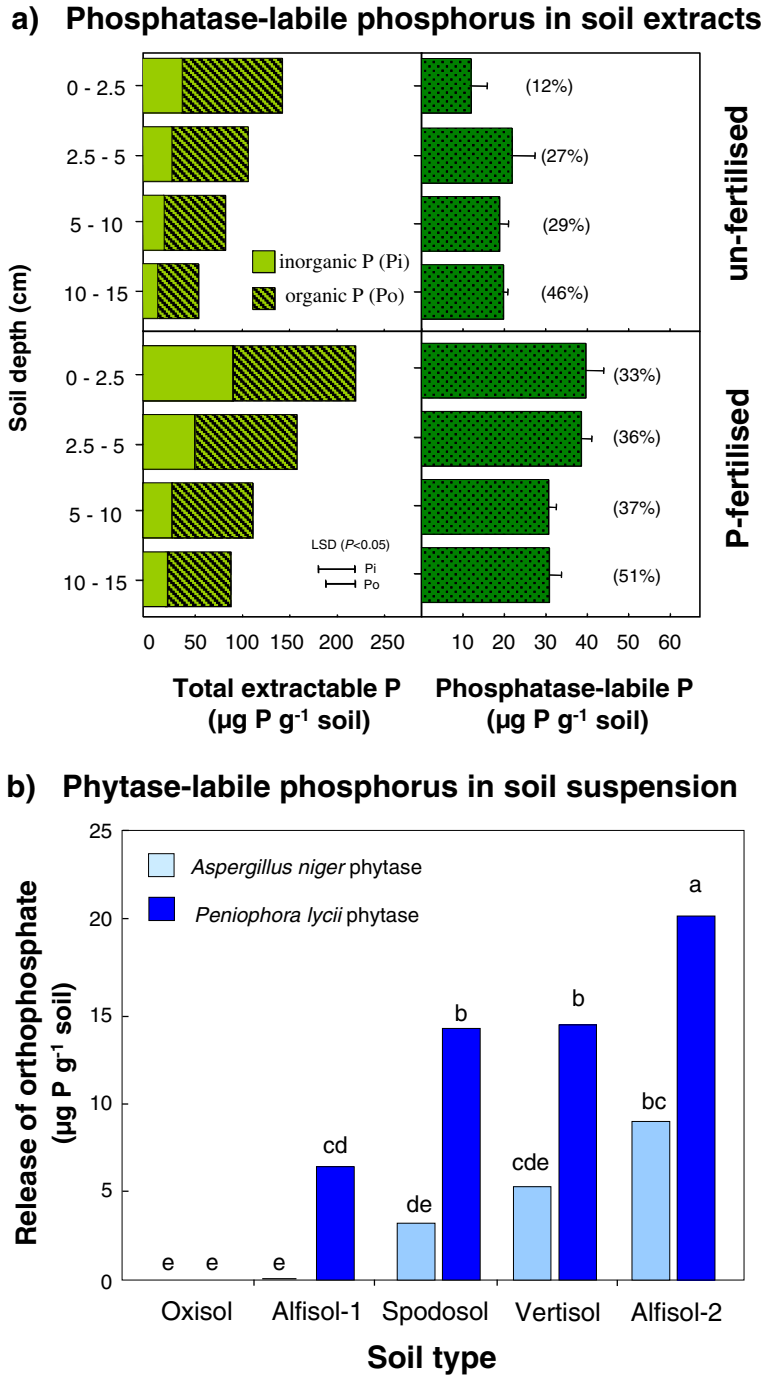


Fig. 8 Phosphatase and phytase-labile phosphorus in soil extracts and suspensions. **a**. Total inorganic and organic phosphorus in sequentially extracted (H_2O; $NaHCO_3$ and NaOH) soil from different depths from a pasture that was either unfertilised or P-fertilised and the amount of phosphatase-labile P in each extract. Data are presented with one standard error or LSD ($P<0.05$) shown as bars and values in parenthesis indicate the % of the extractable P that was amenable to hydrolysis by a non-specific phosphatase/phytase. Data is from George et al. (2007a) **b**. Concentration of phytase labile P in water suspensions (1:10 w:v) of a range of soils (0-10 cm) incubated for 24 h with an excess of *Peniophora lycii* and *Aspergillus niger* phytase. Columns designated with the same letters are not significantly different by LSD ($P<0.05$). Data is from George et al. (2007b)

range of crop and pasture species (e.g. Tadano et al. 1993; Li et al. 1997; Gilbert et al. 1999; Hayes et al. 1999). As a consequence when grown in sterile culture plants are able to utilise organic P supplied in various (e.g. glucose-1-P), but not all organic forms (Hayes et al. 2000b, Richardson et al. 2001b). In other cases, plant utilisation of organic P substrates (e.g. inositol phosphates) was enhanced when the roots were inoculated with cultured soil microorganisms, including a specific isolate of soil bacteria with demonstrable phytase activity (Richardson et al. 2001b). In most instances, root phosphatase activity

is enhanced when plants are grown under P-deficient conditions. This is recognised as a key component of the general response of plants to 'P starvation' (Vance et al. 2003; Richardson et al. 2009b). Phosphatases are thus proposed to play a number of roles that assist plant P nutrition under low P stress including: enhanced recycling of internal P, efficient capture of organic P compounds that may be lost from roots, and access to organic P substrates in soil (Barrett-Lennard et al. 1993; Duff et al. 1994). Consequently, it is commonly believed that enhancing phosphatase activity in roots may assist P-use efficiency. However, there are few examples where selection (or genetic modification) of a species to enhance phosphatase activity has been of clear benefit for P nutrition. For example, George et al. (2008) reported significant variation in the activities of various intra- and extracellular phosphatases (measured against a range of model and actual organic P substrates) for different wheat cultivars, but this did not account for any differences in the P nutrition of the wheat lines when grown in a range of soils with differing organic P content. Access to organic P was considered to be similar for all genotypes irrespective of any differences in their intra- or extracellular phosphatase activities. This raised three questions; (i) was root phosphatase activity already 'sufficient' for utilisation of soil organic P, (ii) were plant-derived phosphatases 'functionally redundant' because the phosphatase activities of soil microorganisms in the rhizosphere were adequate for mobilisation of organic P, or (iii) was acquisition of P from organic P sources by plants constrained by poor availability of organic P substrates in soil (Tarafdar and Claassen 1988)?

Phosphatase activity exuded from roots of various agricultural and tree species can be associated with a depletion of soil organic P (George et al. 2002a; Chen et al., 2004). Chickpea (and some other species) appears to increase the mineralisation of organic P in soil and when intercropped with wheat or maize under controlled conditions is reported to enhance their P nutrition (Li et al. 2003; Li et al. 2004). However, whether enhanced utilisation of organic P occurs as a direct consequence of root or rhizosphere phosphatases, or as an indirect effect of other factors such as root foraging or exudation of organic anions remains unclear.

Although a large proportion of the organic P in soil is poorly characterised, inositol phosphates (isomers and lower order derivatives of inositol hexakisphosphate) generally constitute a significant identifiable component of total organic P. Depending on land use, inositol phosphates typically constitute some to 4–20% of the total organic P, although in some cases they are not detected or may be as high 40% of total organic P (Turner et al. 2002; Turner 2007; Smernik and Dougherty 2007). Inositol phosphates are associated with high molecular weight fractions of soil organic P, are readily adsorbed to soil particles and, depending on pH, react with cations (e.g. Fe and Al in acid soils, and Ca in alkaline soils) to form poorly soluble precipitates (Anderson et al. 1974; Shang et al. 1992; Celi and Barberis 2005). Various studies have demonstrated that plants have limited capability to access P directly from inositol phosphate (Hayes et al. 2000b; Richardson et al. 2001a). This is attributed to poor availability of inositol phosphate in soil solution, low extracellular phosphatase (i.e. phytase) activity in roots, and low efficacy of enzyme-substrate interactions in soil (Richardson et al. 2007; George et al. 2007a). Plant access to P from inositol phosphates in soil is mediated primarily by microorganisms with extracellular phytase activity and their interactions within the rhizosphere (Richardson et al. 2001b; Unno et al. 2005; Richardson and Simpson 2011). Consequently, it has been considered feasible that plants equipped to either 'intercept' inositol phosphates as they are deposited in soil (e.g. in plant materials, animal manures or as a product or microbial metabolism), or to mobilise P from the accumulating pool of inositol phosphates in soil could potentially be used to improve P-use efficiency (Richardson et al. 2007).

Arabidopsis was the first plant species to be genetically modified for release of an extracellular microbial phytase and this enabled the plants to utilise P from inositol phosphate (Richardson et al. 2001a). Other plant species have subsequently been developed for over-expression of phytase and/or phosphatase from different sources (e.g. Lung et al. 2005; George et al. 2004; 2005b; Wasaki et al. 2009; Ma et al. 2009; Wang et al. 2009). Collectively, these studies have shown improved P nutrition of modified plants (compared to control lines) when supplied with organic P sources, albeit generally under controlled growth conditions only and without limitations to substrate availability. In contrast, limited success has been observed when the plants have been evaluated in

soil or in growth conditions where the availability of substrate was restricted, irrespective of total P content (George et al. 2005a, b; Lung and Lim 2006). In addition, interactions between phytases and soil (e.g. deactivation of enzyme activities through adsorption or degradation reactions) may further alter or reduce the efficacy of the enzyme-substrate interactions (Fig. 8b; George et al. 2005c; 2007a) and inositol phosphates adsorbed to soil mineral or clay constituents appear to be protected against enzyme activity (Giaveno et al. 2010). At this stage, it seems necessary to further manipulate the interactions of extracellular enzymes, soil and substrate to achieve enhanced hydrolysis of inositol phosphates by plants. Organic anions improve the mobilisation of organic P in soils and to increase its enzyme-lability, including that of inositol phosphates (Hayes et al. 2000a; Tang et al. 2006; Wei et al. 2010). Further investigation of the capacity of organic anion release from roots to mobilise organic P in soil for interaction with phosphatases is warranted.

Microbial inoculants

Microorganisms play a fundamental role in the biogeochemical cycling of inorganic and organic P in the rhizosphere and detritusphere (Richardson 1994; Whitelaw 2000; Jakobsen et al. 2005b; Harvey et al. 2009; Richardson et al. 2009a; Khan et al. 2010; Richardson and Simpson 2011), with a significant percentage of the total culturable bacterial and fungal communities being reported to have inorganic P-solubilising activity (Kucey et al. 1989; Bowen and Rovira 1999). Rhizosphere microbial inoculants have been proposed as components of integrated nutrient management systems (Adesemoye and Kloepper 2009; Harvey et al. 2009; Khan et al. 2010) with specific interest in their ability to increase the availability of P for crops (Kucey et al. 1989; Bowen and Rovira 1999, Jakobsen et al. 2005b). Research into crop inoculants has focused largely on introducing free-living microorganisms that form non-specific, beneficial associations with a range of plant hosts, that can be mass produced, and have potential to persist in the rhizosphere (e.g. prolific sporulators; Bowen and Rovira 1999; Harvey et al. 2009; Khan et al. 2010). Although symbiotic associations with AM fungi are recognised as playing an important role in the P nutrition of many plants, particularly in low P soils (Smith and Read 2008; Jakobsen et al. 2005b), the inability to readily culture AM fungi in artificial media and lack of establishment of any host plant-specific associations has limited their development as rhizosphere inoculants. By contrast, greater success has been achieved in the utilisation of ectomycorrhizal fungi for inoculation of agro-forestry species (e.g. see Robson et al. 1994).

Most research into the development of microbial inoculants to enhance P availability and root uptake has centred on soil microorganisms capable of solubilising sparingly-available P (Kucey et al. 1989; Whitelaw et al. 1999; Wakelin et al. 2004; Leggett et al. 2007). Bacteria (most commonly *Bacillus* and *Pseudomonas*; Babu-Khan et al. 1995; Richardson and Hadobas 1997; Tye et al. 2002; Taurian et al. 2010, and *Actinomycetes* spp.; El-Tarabily et al. 2008) and fungi (primarily *Penicillium* spp. and *Aspergillus* spp.: Kucey 1983; Relwani et al. 2008; Wakelin et al. 2004; Whitelaw et al. 1999), have been identified as being able to liberate orthophosphate from inorganic and organic substrates under laboratory conditions by releasing organic anions, protons, phosphatases and cation-chelating compounds. However, the main effort to improve P availability using microbial inoculants has focused on P-solubilising fungi and in particular *Penicillium* species (*P. bilaiae* and *P. radicum*: Kucey, 1988; Whitelaw et al. 1999; Leggett et al. 2007; Wakelin et al. 2007). P solubilisation by *Penicillium* spp. has generally been attributed to the release of organic anions (e.g. gluconate, oxalate, citrate) that, as discussed previously, are expected to mobilise soil P (Cunningham and Kuiack 1992; Gadd 1999; Whitelaw et al. 1999). Whilst *Penicillium* spp. are known to mineralise organic forms of P in laboratory media (Yadav and Tarafdar 2003), relatively little is known about the efficacy of their extracellular activities in soil as has been investigated for other fungal enzymes (Fig 8b).

Penicillium species do not appear to exhibit specific plant or soil associations and have been shown to inhabit the rhizosphere of diverse agricultural and non-agricultural plants (Kucey 1983; Hocking et al. 1998; Wakelin et al. 2004; Babana and Antoun 2006; Khan et al. 2008), indicating potential to select and develop inoculants for a broad range of agro-ecological conditions. *P. bilaiae* has been shown to solubilise P in laboratory media (Cunningham and

Kuiack 1992; Takeda and Knight 2006; Wakelin et al. 2004) and improve plant P uptake (Kucey 1988). For example, inoculated wheat obtained up to 18% of its P from sources unavailable to non-inoculated plants under glasshouse conditions (Asea et al. 1988). *P. bilaiae* does not produce any known toxic secondary metabolites (Savard et al. 1994) and stimulates production of root hairs (Gulden and Vessey 2000) and an increase in overall root growth (Vessey and Heisinger 2001). Inoculation with *P. bilaiae* has improved growth of many crop species including wheat (Kucey 1987; Kucey 1988; Anstis 2004), canola (Kucey and Leggett 1989) and grain and pasture legumes (Beckie et al. 1998; Rice et al. 2000). A commercial product based on *P. bilaiae* has been used in North America for at least 15 years and was released in Australia in 2010.

Strains of *Penicillium* spp. capable of solubilising sparingly-available forms of inorganic P have similarly been isolated from Australian cropping soils (*P. radicum*, Whitelaw et al. 1997; *P. bilaiae*, Wakelin et al. 2004). The strain with greatest P-solubilisation efficacy and plant growth promotion was identified as a novel genotype of *P. bilaiae* (Wakelin et al. 2004; Wakelin et al. 2007). Although *P. radicum* was selected for its ability to solubilise inorganic P and improve plant growth (Whitelaw et al. 1997; Whitelaw et al. 1999), further studies showed that the P-solubilisation efficacy by *P. radicum* was significantly lower than that of other *Penicillium* strains, including *P. bilaiae* (Wakelin et al. 2004). The major mechanism of plant growth promotion by *P. radicum* may thus be related to production of plant growth promoting metabolites such as auxins (Anstis 2004), which increase length and density of fine roots and enhance a plant's ability to capture available nutrients without increasing nutrient availability *per se*. Inoculation with *P. bilaiae* also enhanced the production of root hairs and lateral roots (Gulden and Vessey 2000; Vessey and Heisinger 2001) in field peas, and plant growth promotion by a strain of *Penicillium citrinum* is due to the presence of gibberellins (Khan et al. 2008). Synthesis of phytohormones that stimulate root growth therefore provides an indirect mechanism by which rhizosphere microorganisms increase P acquisition and stimulate plant growth (Richardson et al. 2009a).

Opportunities also exist to develop novel 'multi-functional' microbial strains as inoculants, such as P-solubilising and N-fixing strains of *Mesorhizobium mediterraneum* (Peix et al. 2001) and disease biocontrol strains of *Trichoderma harzianum* with capacity to solubilise P (Altomare et al. 1999). Similarly, enhanced plant nutrition and growth may be achieved by using mixtures of plant growth promoting microorganisms. Positive synergistic responses have been observed when cereals (Kucey 1987; Babana and Antoun 2006) and legumes (Osorio and Habte 2001) were inoculated with mixed cultures of *Penicillium* spp. and AM fungi, and for legumes with *Penicillium* and *Rhizobium* spp. (Downey and van Kessel 1990; Rice et al. 2000), with the later also being released as a commercial inoculant.

Although, positive responses to non-symbiotic inoculants are often observed in controlled laboratory and glasshouse experiments, they are observed less consistently in field trials (Goos et al. 1994; Karamanos et al. 2010). For example, analyses by Karamanos et al. (2010) from 26 field sites in Canada between 1989 and 1995 found that inoculation with *P. bilaiae* gave an increase in P uptake and yield of spring wheat in only 5 of 47 trials, despite 33 of the trials showing responses to P fertiliser. Whilst current formulation and seed application technologies were not available at the time, such inconsistencies in field performance still occur and significantly impede the widespread adoption of inoculants in crop and pasture systems. Improved efficacy and ongoing success of rhizosphere inoculants to improve availability of soil P will require appropriate strain formulation and agronomic delivery systems to ensure inoculant survival and improved understanding of factors that may contribute to, or limit, where and when responses may be expected to occur. This work needs to be supported by agronomic and physiological studies to demonstrate effects on plant P uptake, together with ecological studies of inoculants and the soil-borne microbial communities with which they interact (Richardson and Simpson 2011). A thorough understanding of rhizosphere ecology, multi-trophic interactions (Xu 2006; Edel-Hermann et al. 2008) and genetic mechanisms associated with enhancing P-availability in 'responsive' soils will assist selection and targeted deployment of inoculants across farming systems, with potentially greater consistency in performance.

The efficacy of P-solubilising or P-mineralising inoculants depends also on their competitive abilities

in soil environments and capacity to colonise, survive and multiply in the rhizosphere (van Veen et al. 1997; Gyaneshwar et al. 2002). Molecular approaches and DNA-based diagnostics (e.g. real time quantitative PCR) provide new tools for identifying specific taxonomic groups of soil-borne bacteria (Costa et al. 2006) and fungi (Haugland et al. 2004, Sampson et al. 2004; Seifert et al. 2007). Application of such probes for species- and strain-specific identification will allow greater ecological understanding of how inoculants interact with crop roots (i.e. rhizosphere competence), other rhizosphere microbiota and the impacts of management practices on their survival. Molecular genetics also provides opportunity for elucidation of the mechanisms associated with P-solubilisation and plant growth promotion (Gyaneshwar et al. 2002; Rodríguez et al. 2006). Comparative genomic and transcriptomic sequencing of related microbial genotypes with and without P-solubilising capabilities and differential gene expression analyses of strains growing under conditions that require P-solubilisation for growth, have potential to identify enzymes, metabolites and transport proteins involved in these processes. With regard to *Penicillium* spp., comparison of sequence databases (van den Berg et al. 2008; Yuen et al. 2003) will assist with genomic annotation of species with P-solubilising and plant growth promoting functions, potentially leading to new strategies to enhance P availability and use by crop and pasture plants.

Plants that produce more dry matter per unit of phosphorus uptake

Plants with low internal phosphorus requirements

Low internal concentrations of P are characteristic of many non-agricultural plants adapted to low P soils. These plants appear not to be seriously disadvantaged in these low P conditions because they often have high photosynthetic rates per unit leaf area (Lambers et al. 2010). Low leaf P concentrations are partly due to a scleromorphic leaf anatomy and high leaf mass per unit leaf area (LMA). However, P content per unit leaf area may not be extremely low and this partly explains how high photosynthetic rates per unit leaf area are achieved. For example, in *Banksia* spp. adapted to low soil P, photosynthetic rate per unit of leaf P (photosynthetic P-use efficiency) is higher than in most other species (Denton et al. 2007; Lambers et al. 2010). The mechanisms behind high photosynthetic P-use efficiency and the possible association with high LMA deserve further investigation. High LMA reduces the ability of plants to achieve high growth rates (Lambers & Poorter 1992) and this would be undesirable in crop plants. For woody long lived plants, traits associated with high LMA and efficient mobilisation of P from senescing leaves are key factors in the long lifespan of leaves and efficient use of P at the whole plant level, as they increase the residence time of P in the plant (Denton et al. 2007).

There are examples of species used in agriculture that also have low internal P concentrations. For example, Hill et al. (2005) observed that among pasture grasses (i.e. herbaceous shorter lived plants than those described above), two native Australian species (wallaby grass; *Austrodanthona richardsonii* (Cashmore) H.P.Linder and weeping grass; *Microlaena stipoides* (Labill.) R.Br.) had internal critical P concentrations that were 30–45% less than those of a range of introduced pasture grasses with equivalent relative growth rates. However, across all of the grasses examined there was no relationship between the critical external P concentrations (a relative measure of the P fertiliser requirements) and their critical internal P concentrations. This is not unusual for interspecific comparisons and is considered to reflect slow diffusion of P in soils and, consequently, the high importance of traits that enhance foraging by root systems under low P conditions (Nye 1973; Silberbush and Barber 1983).

In intraspecific comparisons there is clear evidence for variation in internal P-use efficiency under both glasshouse and field conditions. For instance, in a comparison of 14 *Brassica* cultivars, grown at a range of P supplies in hydroponics, a two-fold difference was found in total biomass production at both low- and high-P supply (Akhtar et al. 2008). P-efficient cultivars produced most shoot and total biomass and had the lowest shoot P concentrations. One aspect of P-use efficiency in these plants was translocation of P from metabolically inactive sites to active sites in non-mature tissues (Akhtar et al. 2008).

In many species, a large fraction of the P in leaves of plants grown with high-P supply tends to be orthophosphate (e.g. 75% in barley leaves; Chapin and Bieleski 1982), located mostly in the vacuole

(Foyer and Spencer 1986). Thus, it is expected that leaves can function equally well at significantly reduced leaf P concentrations. Indeed, tomato plants exhibited the same relative growth rate (RGR) at 5 mg P g^{-1} DM as at 10 mg P g^{-1} DM (De Groot et al. 2001). However, at still lower leaf P concentrations, leaf area ratios (LAR), net assimilation rates (NAR) and RGR decline, with changes in LAR being more important at mild P limitation and changes in NAR being more important at more severe P limitation. The increase in leaf starch concentrations at mild P limitation shows that reductions in RGR and LAR are due primarily to effects on leaf area expansion, rather than the result of limitation by assimilate supply (Brooks 1986; Rao and Terry 1989; De Groot et al. 2001). Strong reductions in photosynthesis at severely limiting P supply (De Groot et al. 2003) have also been found for spinach (*Spinacia oleracea* L.; Brooks 1986) and barley (Fay et al. 1996).

Further evidence for variation in internal P-use efficiency of crop plants comes from significant variation in shoot mass per unit P uptake in a comparison of 376 *Brassica oleracea* L. accessions plus 74 commercial cultivars grown at a range of soil P concentrations (Hammond et al. 2009). Similarly, in a glasshouse comparison of 73 bread wheat and durum wheat genotypes there was considerable variation in shoot dry weight at similar concentrations of shoot P (Ozturk et al. 2005). These studies and that of Vesterager et al. (2006) with 21 genotypes of pigeon pea (*C. cajan*), suggest there is useful variation in internal P-use efficiency of crop species, in addition to variation in efficiency for P acquisition. However, it is important to ensure that reduction in the P concentrations of plant tissues are not traded off against other desirable traits. Presumably, low plant P concentrations can be achieved by reducing the concentrations of inorganic P in vacuoles or by enhancing mobilisation of P from metabolically inactive to active tissues. However, lower investment in other compounds (e.g. ribosomal RNA, a major component of the nucleotide P fraction and about 80% of the total RNA pool: Warner et al. 2001; Perry 2007) may slow rates of protein synthesis and growth (Matzek and Vitousek 2009).

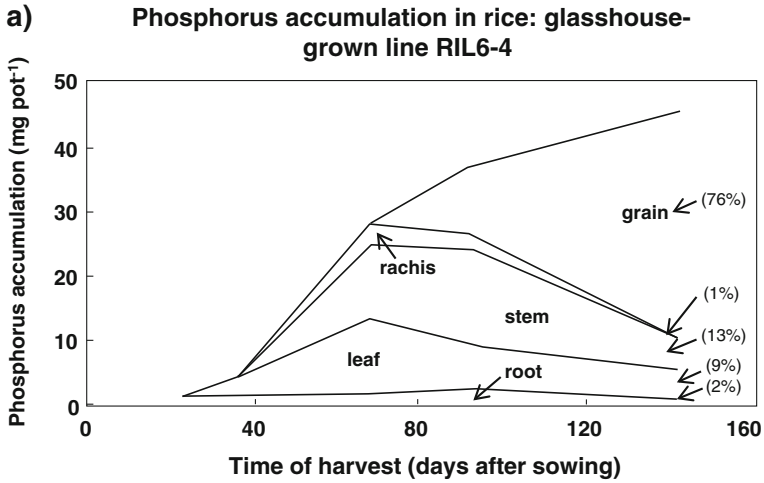
The expected end-use of a plant will also influence the feasibility of reducing internal P concentration of plant tissues. The potential for selecting pasture plants with lower internal P requirements has been examined on a number of occasions and it is generally agreed that there is a reasonable prospect for reducing the P concentration of herbage by breeding (e.g. Godwin and Wilson 1976). For legume-based pastures, the target for improvement must be the legume component for efficiency in the P-balance and fertiliser costs of the pastures to be achieved (Simpson et al. 2011). However, the critical P concentrations of many pasture species (Pinkerton et al. 1997) are already relatively close to the P concentrations needed in ruminant feeds for growing and lactating animals (e.g. Ozanne 1980; Freer et al. 2007) and that of senescing and dead herbage or unfertilised pasture is often less than required for grazing ruminant production (e.g. McIvor et al. 2011). This casts doubt on the wisdom of attempting to improve P-efficiency by selecting for forages with lower internal P concentrations.

Manipulation of plant P translocation and reduced export of P by crops

Crop plants with improved internal plant P-use efficiency would produce more dry matter per unit of P taken up by the plant, thereby reducing the amount of P fertiliser required per unit of yield. It seems logical that P fertiliser requirements could be further reduced if less of the P contained in the plant were to leave the farm in harvested material.

Cropping systems often have a relatively high P-balance efficiency (45–55% of P applied is exported in grain, McLaughlin et al. 1992; Weaver and Wong 2011) and require large inputs of P fertiliser. High P removal results from P contained in harvested material (grain, seeds and fruits), with relatively small proportions remaining in stems and roots (Fig. 9a; Rose et al. 2007; Rose et al. 2010). The P-harvest index of cereals is generally higher than 50% and sometimes up to 90% for field grown crops in Australia (Batten and Khan 1987; Zubaidi et al. 1999; Santonoceto et al. 2002; Ryan and Angus 2003) and similarly ranged from 57% to 86% for various rice genotypes grown in the field (Fig. 9b; Rose et al. 2010). However, for reasons of practicality, P-harvest index calculations usually do not consider that P can be retained in roots, which can be variable. Rose et al. (2007) reported roots contained 6–11% (canola) and 22% (wheat) of plant P at maturity, whereas for glasshouse grown rice it constituted about 2% (Fig. 9a). Proportionately more P is mobilized in

a)



b)

Variation in yield and grain phosphorus: 37 field-grown genotypes

Yield component	mean	range
Grain yield (g plant^{-1})	84.1	41.5 - 163.4
Total plant biomass (g plant^{-1})	166.4	88.8 - 290.5
Harvest index (HI; % biomass in grain)	50.3	36.8 - 62.8
Grain P content (mg plant^{-1})	221	115 - 439
Total plant P uptake (mg plant^{-1})	279	143 - 522
P harvest index (PHI: % P in grain)	78.7	57.0 - 85.9
Harvest index ratio (PHI:HI)	1.58	1.34 - 2.00
Grain P concentration (mg g^{-1})	2.63	1.94 - 3.18

Fig. 9 **a**. Accumulation and distribution of phosphorus (P) in organs of rice plants (line RIL6-4) grown to maturity under glasshouse conditions. Data are the mean of 3 replicates and values shown in parenthesis indicate the percentage distribution of P across different tissues at harvest. **b**. Plant and grain biomass and plant and grain P uptake for 37 traditional and modern rice genotypes grown to maturity under field conditions. Values are presented as the mean for 3 replicates for each genotype and is shown as the mean and range across all genotypes. Grain P concentration and harvest index for both biomass (HI) and P content (PHI) of grain are also presented. Data is from Rose et al. (2010)

P-starved than in P-sufficient plants (Elliot et al. 1997), although P-harvest index may also be reduced by factors that reduce grain harvest index such as dry spring periods or disease (Zubaidi et al. 1999). In the study by Rose et al. (2010), P harvest index was highly correlated with grain harvest index suggesting that exploiting genetic variability for this trait may be counterproductive. On the other hand, grain P concentration varied widely from 1.94 mg P g^{-1} to 3.18 mg P g^{-1} across genotypes (Fig. 9b). Importantly this variation in grain P percentage was not associated with either smaller seed size or reduction in grain yield and showed no significant correlation with harvest index. This suggests that low seed P concentration may be a suitable criterion for breeding more P-efficient rice through a reduction in the export of P from fields at harvest (Rose et al. 2010). However, low P in grain and seed can impact on subsequent seedling vigor (Bolland and Baker 1988; De Marco 1990; Thomson and Bolger 1993) and agronomic interventions (e.g. P seed priming; Sekiya and Yano 2010) may be required to overcome any restrictions to early seedling growth. Moreover, the genetic basis of P translocation efficiency within plants and its remobilisation to grain requires more detailed investigation.

Opportunity exists also for manipulation of the P composition of grains. P concentrated in the seed of crops is mostly in the form of phytate, a mixed cation salt of phytic acid, and there has been some effort to reduce the phytate content of common cereals (Raboy 2003). High phytate grains do not provide adequate P for intensive pig and poultry production necessitating P supplementation or addition of phytase to feeds (Raboy 2009). High phytate content of grains and fruits also contributes to a number of nutritional problems for humans including poor availability of essential micronutrients such as zinc (Zn), Ca and Fe (Kumar et al. 2010). For example, Ryan et al. (2008)

found that Zn bioavailability in whole-wheat grain was low, and became extremely low when P fertiliser was used. This was attributed to a combination of both higher phytic acid content and lower Zn concentrations. On the contrary, dietary phytate may also play an important role for improving digestive health in human diets (Watt et al. 2001; Kumar et al. 2010).

Effort to select low phytic acid grain crops has to date largely been directed at modification of animal feeds where there is clear advantage for improving access to dietary P and potential for reducing the P content in animal waste streams (Raboy 2009; Rasmussen et al. 2010). Mutations in numerous genes involved in the metabolism of phytic acid have been identified and characterised among plant species, including barley (*H. vulgare*), maize (*Z. mays*), rice (*O. sativa*), potato (*Solanum tuberosum* L.) and soybean (*G. max*) (Rasmussen et al. 2010). However, the seed P concentration of the current low phytic acid mutants is generally little changed from their high phytate parents due to seed phytate being replaced by inorganic P (Raboy 2009). For instance, a low phytic acid wheat mutant had 43% less phytic acid in the bran, but the bran total P concentration was reduced by only 12% and total P in other milling fractions actually increased (Guttieri et al. 2004). Nonetheless, the development of low phytic acid mutants indicates that seed P characteristics can be manipulated and Raboy (2009) speculates that an alternative way to address the development of low P grains could be to aim for plants with low total seed P, but with no change in the proportion of seed P that consists of phytate.

To ensure that selection of plants for low total seed P also reduces crop P fertiliser requirements, it will be important to ensure that efficient mobilisation of P to seeds and high-P harvest indices are maintained (Fig. 9; Rose et al. 2010). At this stage, it is unclear whether P retained in crop stubble and roots would be cycled effectively to ensure that the reduced export of P would translate into a reduced fertiliser requirement. When farmgate P-balance efficiency is calculated for Australian farming systems on soils with high P-sorption capacity, poor efficiency is almost invariably associated with agricultural industries that export relatively low amounts of P in products (e.g. grazing enterprises: McLaughlin et al. 1992; Weaver and Wong 2011). The reasons for this are not well understood, but the accumulations of sparingly-available organic and inorganic P in these soils may, in part, reflect high rates of return of P in plant material and animal waste to the soil (Simpson et al., 2011).

Conclusions and future prospects

Plant breeding issues

Screening large numbers of genotypes that are adapted to low P fertility (e.g. common bean, Singh et al. 1989) or able to respond to fertiliser application (e.g. white clover; *Trifolium repens* L.; Caradus and Dunn 2000) has in a some cases proven to be relatively unproductive, or to result in slow genetic progress when field conditions are not optimal (e.g. Górny and Sodkiewicz 2001). In the case of white clover, P-efficiency (measured as response to applied P) was shown to be heritable under glasshouse conditions (Caradus et al. 1992; Caradus 1994) but differences in response under field conditions were minimal (Caradus and Dunn 2000). Lynch (2007) has argued that field screening of genotypes for low fertility adaptation (P uptake efficiency) *per se*, is likely to be unproductive. This is because of confounding influences of spatial variation in soil properties (including nutrients, soil acidity, compaction), which can restrict root growth, effects of environmental interactions including light and soil moisture that can influence P-stress severity, and biotic stresses that affect root growth and function such as nematodes and root rots. It is suggested that a better strategy to achieve rapid genetic progress is to identify genotypes that have root traits useful for efficient P acquisition and to then incorporate these traits into elite lines by introgression using, where possible, marker assisted selection.

To date, selection for root architectural traits has been used to develop P-efficient genotypes of bean and soybean that are being deployed in Africa, Asia, and South America (Lynch 2007). The identification of specific root traits enhancing P acquisition has greatly facilitated genotype screening and crossing. Many of these traits can be evaluated directly in early seedling screens or by direct phenotypic assessment in the field. Comparable traits have been identified in maize (Zhu et al. 2005a) and feature as the most likely

factor associated with improved P uptake by wheat (Manske et al. 2000; Liao et al. 2008) demonstrating their importance in a range of annual crops. It appears potentially feasible to develop new cultivars that combine P-efficient root traits (e.g. root length density in wheat, Manske et al. 2000) with internal P-efficiency (wheat with low internal P requirements, Ozturk et al. 2005) and reduced P-export from farms (Rose et al. 2010). However, the effort required to combine multiple P-efficiency traits into elite cultivars that are agronomically and commercially acceptable should not be underestimated.

By contrast, there are few examples where P-uptake by soil-grown plants is improved as a result of incorporating organic anion or phosphatase secretion from roots. The case for these traits, based on the attributes of natural plants that utilise specialist P-efficiency mechanisms, is compelling and is backed by demonstrations that P can be mobilised from sparingly-available pools in soils when treated with organic anions, phosphatases (Figs. 7 and 8) or microbial inoculants. However, instances of genetic modification of plants to enhance organic anion or phosphatase secretion from roots, whilst successful under in some controlled laboratory studies, have proven to be difficult to repeat or have shown variable success when evaluated in soil. The need for a better understanding of trait interactions and the ecophysiology of the rhizosphere is emerging as an important factor in development of improved plants via these P-efficiency routes (George and Richardson 2008).

Trait interactions and tradeoffs

Similar knowledge gaps to those already mentioned obstruct wider adoption of P-efficiency root traits as selection criteria in plant breeding programs. Information is needed about how traits interact to form integrated phenotypes, metabolic and ecological tradeoffs associated with trait expression and how specific root traits influence interplant competition (George and Richardson 2008). Consequently, it is proving just as important to research potential trait interactions and tradeoffs to pave the way for successful plant breeding and genetic manipulation.

Currently we have a limited understanding of the interaction of traits related to P acquisition, despite the importance of trait interactions for whole plant performance. The large number of possible trait interactions and therefore integrated phenotypes (e.g. five traits each existing in two states would result in 2^5, or 32 integrated phenotypes) makes simulation modelling an attractive tool. Plants colonised by AM fungi are known to display altered root morphology and architecture (e.g. lower root hair frequency and length, less branching; Kothari et al. 1990; Hetrick 1991) although the impact of this on progress in selecting for improved root systems is unknown. Root architectural traits, themselves, may interact to alter the extent of inter-root competition, which is an important component of overall root foraging efficiency (Ge et al. 2000; Rubio et al. 2003; Rubio et al. 2001; Walk et al. 2006).

Root strategies for P acquisition may be synergistic or antagonistic. An example of trait synergy in P acquisition is the interaction of four distinct root hair traits, whose combined effect on P acquisition was predicted by modelling to be 371% greater than their additive effects (Ma et al. 2001b). Traits such as root hairs and root exudates may also have synergism with root architectural traits, which locate root axes in soil domains with varying P availability. For example, longer root hairs would be expected to provide greater benefit to the plant if they were positioned in P-rich topsoil as opposed to P-poor subsoil. Phosphatases that mobilise P from soil organic matter would be more useful if exuded by shallow roots than by deep roots, since in most soils organic matter content decreases with depth.

Trait interactions and their ecophysiological context is an important consideration when breeding for P-efficiency. For example, comparisons of long (0.31 mm) and short root hair (0.20 mm) selections of white clover (*T. repens* cv. Tamar) showed no P-uptake benefit from the longer root hairs unless the plants were grown in the absence of AM fungi (Caradus 1981). This is despite clear improvement in P acquisition as a consequence of longer root hairs on roots of monocots and dicots (Gahoonia and Nielsen 1997; 2004; Wang et al. 2004; Yan et al. 2004; Zhu et al. 2010b). Schweiger et al. (1995) observed that P-uptake benefits of AM fungi were greatest for plants with short root hairs. Their results suggest that root hairs would need to have been at least 2-fold (or more) longer than the length achieved by divergent selection in white clover to realise a P-uptake advantage over that already conferred by the symbiotic AM relationship. It may also be significant

that the positive correlations between root hair length and P acquisition mentioned above, including where roots were colonised by mycorrhiza (Baon et al. 1994; Miguel 2004), were observed for plants with relatively long root hairs (range 0.5–1.7 mm). The implications for white clover improvement may be that if variation in root hair length is limited and plants cannot be selected with root hairs longer than around 0.5 mm, selection for alternative root traits such as long, fine roots may be a more successful way to improve P-use efficiency (e.g. Crush et al. 2008).

The utility of a particular trait for plants in low P environments must also take into account potential tradeoffs of the trait with other plant processes. The most obvious tradeoff for many traits is the opportunity costs of diverting carbon and other resources from specific functions. The value of 'low cost' root foraging options has already been discussed. Organic anion (e.g. Dinkelaker et al. 1989; Lambers et al. 2006) and AM fungal strategies (e.g. Graham and Miller 2005) are potentially energy intensive ways to acquire P. Attempts to increase organic anion secretion in crop species that are colonized by AM fungi may establish interesting dilemmas for carbon allocation. In natural ecosystems, these two P-efficiency strategies are hypothesised to have been deployed according to degree of soil P deficiency under which plants have evolved, with organic anion secretion by cluster roots (P-mining) being used by plants in severely P-impoverished landscapes and AM fungal colonisation of roots (P-scavenging) more frequent in plants from moderately low P environments (Lambers et al. 2008, 2010). For many species, the tendency is to either deploy cluster roots and organic anion secretion or to be colonised by AM fungi, but a limited number of species (e.g. *Casuarina* spp. and possibly other actinorhizal species) deploy both P-efficiency traits (Lambers et al. 2006). Therefore, attempts to incorporate a capacity for increased organic anion secretion into crop species has natural precedence. How the traits interact in a single plant is unknown, but both organic anion secretion and AM fungal colonisation are reduced by plants when soil P availability is improved (Reddell et al. 1997) suggesting that it may be costly to unnecessarily deploy such traits.

Agroecosystems are managed environments and the P-efficiency traits most suited to one form of agricultural management may not be the best fit for an alternative management system. For example, George et al. (2011) found that the appropriate mix of genetic components that contribute to variation in P nutrition of barley differed under alternative cultural conditions (i.e. conventional vs minimum tillage). They concluded that in some cases the large interaction between genetic and environmental (GxE) variables may limit the usefulness of specific P-use efficiency traits to the conditions under which screening for P-efficiency had been performed; thus highlighting the importance of GxExM (management) interactions. Because of the heterogeneity of soils, tradeoffs can also result if exploitation of one soil domain reduces exploitation of another with its attendant resources. For example, an important tradeoff or opportunity cost to topsoil foraging is increased sensitivity to drought stress, since water is located deep in the soil profile in many environments. A comparison of deep rooted and shallow rooted bean genotypes showed that while shallower genotypes had superior growth under P stress, deep rooted genotypes had superior growth under water stress (Ho et al. 2005). A potential breeding solution to this problem is the development of architectural multilines composed of closely related genotypes having identical shoot traits but contrasting root architectures (Henry et al. 2010b). The validity of such an approach, however, remains to be adequately verified under field conditions. Some native plant species adapted to low P and drought prone environments have resolved this issue by developing dimorphic root systems (Jeschke and Pate 1995; Shane et al. 2005).

System impacts

An obvious concern with the introduction of P-mining practices or more P-efficient crop genotypes is the possibility of soil mining and gradual depletion of soil fertility, especially in low input systems (e.g. Lynch 2007; Sánchez 2010; McIvor et al. 2011). This is probably less of a problem where novel genotypes are being introduced as part of a wider scheme to reduce P-removals and to protect the sustainability of the production system. However, it is suggested that other agro-ecological and socio-economic system level benefits of P-efficiency can mitigate some of the risk of P depletion. For example, P extraction by genotypes with better root traits may be balanced by reduced soil erosion created by increased shoot biomass (Henry et al. 2010a). Simpson et al. (2011)

discuss in more detail how agroecosystem level issues can also have a large impact on the success of attempts to utilise P-efficient plants and highlight the need to understand the ecology of nutrient acquisition in crops, plant communities and the rhizosphere for successful outcomes.

Acknowledgements The authors thank Mark Conyers, Peter Cornish, Keith Helyar and Peter Randall for critical discussion of the ideas expressed in this paper. FAS and SES wish to acknowledge the Australian Research Council, the South Australian Grain Industry Trust and the Waite Research Institute for research support and AO thanks Else Bünemann and Emmanuel Frossard for stimulating discussions. Preparation of the review was funded in part by Meat and Livestock Australia Ltd and CSIRO's National Research Flagships Program's Flagship Collaboration Fund which aims to enhance collaboration between CSIRO's Flagships, Australian universities and other publicly-funded research agencies.

References

Abdolzadeh A, Wang X, Veneklaas EJ, Lambers H (2010) Effects of phosphorus supply on growth, phosphate concentration and cluster-root formation in three *Lupinus* species. Ann Bot 105:365–374

Adams MA, Pate JS (1992) Availability of organic and inorganic forms of phosphorus to Lupins (*Lupinus* spp). Plant Soil 145:107–113

Adams MA, Bell TL, Pate JS (2002) Phosphorus sources and availability modify growth and distribution of root clusters and nodules of native Australian legumes. Plant Cell Environ 25:837–850

Adesemoye AO, Kloepper JW (2009) Plant-microbes interactions in enhanced fertilizer-use efficiency. Appl Microbiol Biotechnol 85:1–12

Ae N, Arihara J, Okada K (1991) Phosphorus uptake mechanisms of pigeon pea grown in alfisols and vertisols. In: Johansen C, Lee KK, Sahrawat KL (eds) Phosphorus nutrition of grain legumes in the semi arid tropics. ICRISAT, Andra Pradesh, pp 91–98

Akhtar MS, Yoko O, Tadashi A (2008) Intraspecific variations of phosphorus absorption and remobilization, P forms, and their internal buffering in *Brassica* cultivars exposed to a P-stressed environment. J Integr Plant Biol 50:703–716

Altomare C, Norvell WA, Björkman T, Harman GE (1999) Solubilization of phosphates and micronutrients by the plant-growth-promoting and biocontrol fungus *Trichoderma harzianum* Rifai 1295–22. Appl Environ Microbiol 65:2926–2933

Anderson G, Williams EG, Moir JO (1974) A comparison of the sorption of inorganic orthophosphate and inositol hexaphosphate by six acid soils. J Soil Sci 25:51–62

Anoop VM, Basu U, McCammon MT, McAlister-Henn L, Taylor GJ (2003) Modulation of citrate metabolism alters aluminum tolerance in yeast and transgenic canola over-expressing a mitochondrial citrate synthase. Plant Physiol 132:2205–2217

Anstis ST (2004) *Penicillium radicum*: Studies on the mechanisms of plant growth promotion in wheat. PhD thesis, The University of Adelaide, Australia

Asea PEA, Kucey RMN, Stewart JWB (1988) Inorganic phosphate solubilisation by two *Penicillium* species in solution culture and soil. Soil Biol Biochem 20:459–464

Asmar F, Gahoonia TS, Nielsen NE (1995) Barley genotypes differ in activity of soluble extracellular phosphatase and depletion of organic phosphorus in the rhizosphere soil. Plant Soil 172:117–122

Babana AH, Antoun H (2006) Effect of Tilemsi phosphate rock-solubilizing microorganisms on phosphorus uptake and yield of field-grown wheat (*Triticum aestivum* L.) in Mali. Plant Soil 287:51–58

Babu-Khan S, Yeo TC, Martin WL, Duron MR, Rogers RD, Goldstein AH (1995) Cloning of a mineral phosphate-solubiliizing gene from *Pseudomonas cepacia*. Appl Environ Microbiol 61:972–978

Baon JB, Smith SE, Alston AM (1993) Mycorrhizal responses of barley cultivars differing in P efficiency. Plant Soil 157:97–105

Baon JB, Smith SE, Alston AM (1994) Growth-response and phosphorus uptake of rye with long and short root hairs—interactions with mycrorrhizal infection. Plant Soil 167:247–254

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

Barrow NJ (1980) Evaluation and utilisation of residual phosphorus in soils. In: Khasawneh FE, Sample EC, Kamprath EJ (eds) The role of phosphorus in agriculture. American Society of Agronomy, Madison, pp 333–339

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

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

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

Batten GD, Khan MA (1987) Uptake and utilisation of phosphorus and nitrogen by bread wheats grown under natural rainfall. Aust J Exp Agric 27:405–410

Beckie HJ, Schlechte D, Moulin AP, Gleddie SC, Pulkinen DA (1998) Response of alfalfa to inoculation with *Penicillium bilaii* (Provide). Can J Plant Sci 78:91–102

Beebe SE, Rojas-Pierce M, Yan X, Blair MW, Pedraza F, Muñoz F, Tohme J, Lynch JP (2006) Quantitative trait loci for root architecture traits correlated with phosphorus acquisition in common bean. Crop Sci 46:413–423

Begum HH, Osaki M, Shinano T, Miyataki H, Wasaki J, Yamamura T, Watanabe T (2005) The function of a maize-derived phosphoenolpyruvate carboxylase in phosphorus-deficient transgenic rice. Soil Sci Plant Nutr 51:497–506

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

Bolan NS (1991) A critical review on the role of mycrorrhizal fungi in the uptake of phosphorus by plants. Plant Soil 134:189–207

Bolland MDA, Baker MJ (1988) High phosphorus concentrations in seed of wheat and annual medic are related to higher rates of dry matter production of seedlings and plants. Aust J Experim Agric 28:765–770

Bonser AM, Lynch J, Snapp S (1996) Effect of phosphorus deficiency on growth angle of basal roots in *Phaseolus vulgaris*. New Phytol 132:281–288

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

Bouldin DR (1961) Mathematical description of diffusion process in the soil. Soil Sci Soc Am Proc 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

Bouwman AF, Beusen AHW, Billen G (2009) Human alteration of the global nitrogen and phosphorus soil balances for the period 1970-2050. Global Biogeochem Cycles 23: GB0A04. doi:10.1029/2009GB003576

Bowen GD, Rovira AD (1999) The rhizosphere and its management to improve plant growth. Adv Agron 66:1–102

Brooks A (1986) Effects of phosphorus nutrition on ribulose-1,5-bisphosphate carboxylase activation, photosynthetic quantum yield and amounts of some Calvin-cycle metabolites in spinach leaves. Func Plant Biol 13:221–237

Bünemann EK (2008) Enzyme additions as a tool to assess the potential bioavailability of organically bound nutrients. Soil Biol Biochem 40:2116–2129

Burkitt LL, Small DR, McDonald JW, Wales WJ, Jenkin ML (2007) Comparing irrigated, biodynamic and conventionally managed dairy farms. 1. Soil and pasture properties. Aust J Experim Agric 47:479–488

Caradus JR (1981) Effect of root hair length on white clover growth over a range of soil phosphorus levels. New Zeal J Agric Res 24:353–358

Caradus JR (1994) Selection for improved adaptation of white clover to low phosphorus and acid soils. Euphytica 77:243–250

Caradus JR, Dunn A (2000) Adaptation to low fertility hill country in New Zealand of white clover lines selected for differences in response to phosphorus. New Zeal J Agric Res 43:63–69

Caradus JR, Mackay AD, Wewala S, Dunlop J, Hart A, van den Bosch J, Lambert MG, Hay MJM (1992) Inheritance of phosphorus response in white clover. Plant Soil 146:199–208

Celi L, Barberis E (2005) Abiotic stabilization of organic phosphorus in the environment. In: Turner BL, Frossard E, Baldwin D (eds) organic phosphorus in the environment. CABI Publishing, Wallingford, pp 113–132

Chapin FS, Bieleski RL (1982) Mild phosphorus stress in barley and a related low-phosphorus-adapted barley grass: Phosphorus fractions and phosphate absorption in relation to growth. Physiol Plantarum 54:309–317

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

Chen CR, Condron LM, Turner BL, Mahieu N, Davis MR, Xu ZH, Sherlock RR (2004) Mineralisation of soil orthophosphate monoesters under pine seedlings and ryegrass. Aust J Soil Res 42:189–196

Cherr CM, Scholberg JMS, McSorely R (2006) Green manure approaches to crop production: a synthesis. Agron J 98:302–319

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

Condron LM (2004) Phosphorus—surplus and deficiency. In: Schjønning P, Christensen BT, Elmholt S (eds) Managing Soil Quality—challenges in modern agriculture. CAB International, Wallingford, pp 69–84

Cordell D, Drangert JO, White S (2009) The story of phosphorus: Global food security and food for thought. Global Environ Chang 19:292–305

Costa R, Salles, JF, Berg G, Smalla K (2006) Cultivation-independent analysis of *Pseudomonas* species in soil and in the rhizosphere of field-grown *Verticillium dahliae* host plants. Environ Microbiol 8:2136–2149

Crush JR, Boulesteix-Coutelier ARL, Ouyang L (2008) Phosphate uptake by white clover (*Trifolium repens* L.) genotypes with contrasting root morphology. New Zeal J Agric Res 51:279–285

Cunningham JE, Kuiack C (1992) Production of citric and oxalic acids and solubilization of calcium phosphate by *Penicillium billai*. Appl Environ Microbiol 52:1451–1458

De Groot CC, Marcelis LFM, Van Den Boogaard R, Lambers H (2001) Growth and dry-mass partitioning in tomato as affected by phosphorus nutrition and light. Plant Cell Environ 24:1309–1317

De Groot CC, Van den Boogaard R, Marcelis LFM, Harbinson J, Lambers H (2003) Contrasting effects of N and P deprivation on the regulation of photosynthesis in tomato plants in relation to feedback limitation. J Exp Bot 54:1957–1967

de la Fuente JM, Ramírez-Rodríguez V, Cabrera-Ponce JL, Herrera-Estrella L (1997) Aluminum tolerance in transgenic plants by alteration of citrate synthesis. Science 276:1566–1568

De Marco DG (1990) Effect of seed weight, and seed phosphorus and nitrogen concentrations on the early growth of wheat seedlings. Aust J Exp Agric 30:545–549

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

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

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

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

Delhaize E, Taylor P, Hocking PJ, Simpson RJ, Ryan PR, Richardson AE (2009) Transgenic barley (*Hordeum vulgare* L.) expressing the wheat aluminium resistance gene (*TaALMT1*) shows enhanced phosphorus nutrition and grain production when grown on an acid soil. Plant Biotechnol J 7:391–400

Denton MD, Veneklaas EJ, Freimoser FM, Lambers H (2007) *Banksia* species (Proteaceae) from severely phosphorus-impoverished soils exhibit extreme efficiency in the use and re-mobilization of phosphorus. Plant Cell Environ 30:1557–1565

Dessureault-Rompre J, Nowack B, Schulin R, Luster J (2007) Spatial and temporal variation in organic acid anion exudation and nutrient anion uptake in the rhizosphere of *Lupinus albus* L. Plant Soil 301:123–134

Dinkelaker B, Romheld BV, Marschner H (1989) Citric acid excretion and precipitation of Ca citrate in the rhizosphere of white lupin (*Lupinus albus* L.). Plant Cell Environ 12:285–292

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

Downey J, van Kessel C (1990) Dual inoculation of *Pisum sativum* with *Rhizobium leguminosarum* and *Penicillium bilaji*. Biol Fert Soils 10:194–196

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

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

Durrett TP, Gassmann W, Rogers EE (2007) The FRD3-mediated efflux of citrate into the root vasculature is necessary for efficient iron translocation. Plant Physiol 144:197–205

Edel-Hermann V, Gautheron N, Alabouvette C, Steinberg C (2008) Fingerprinting methods to approach multitrophic interactions among microflora and microfauna communities in soil. Biol Fert Soils 44:975–984

Elliot DE, Reuter DJ, Reddy GD, Abbott RJ (1997) Phosphorus nutrition of spring wheat (*Triticum aestivum* L.) 1. Effects of phosphorus supply on plant symptoms, yield, components of yield, and plant phosphorus uptake. Aust J Agric Res 48:855–867

El-Tarabily KA, Nassar AH, Sivasithamparam K (2008) Promotion of growth of bean (*Phaseolus vulgaris* L.) in a calcareous soil by a phosphate-solubilizing, rhizosphere-competent isolate of *Micromonospora endolithica*. Appl Soil Ecol 39:161–171

Eshel A, Nielsen KL, 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. IACR-Long Ashton Research Station Bristol, England, p 63

Fageria NK (2007) Green manuring in crop production. J Plant Nutr 30:691–719

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

Fay P, Mitchell DT, Osborne BA (1996) Photosynthesis and nutrient-use efficiency of barley in response to low arbuscular mycorrhizal colonization and addition of phosphorus. New Phytol 132:425–433

Fox TR, Comerford NB, McFee WW (1990) Phosphorus and aluminium release fom a spodic horizon mediated by organic acids. Soil Sci Soc Am J 54:1763–1767

Foyer C, Spencer C (1986) The relationship between phosphate status and photosynthesis in leaves. Planta 167:369–375

Freer M, Dove H, Nolan JV (2007) Nutrient requirements of domesticated ruminants. CSIRO Publishing, Collingwood

Gadd GM (1999) Fungal production of citric and oxalic acid: Importance in metal speciation, physiology and biogeochemical processes. Advan Microbial Physiol 41:47–92

Gahoonia TS, Nielsen NE (1992) The effect of root induced pH changes on the depletion of inorganic and organic phosphorus in the rhizosphere. Plant Soil 143:185–191

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

Gahoonia TS, Nielsen NE (1998) Direct evidence on participation of root hairs in phosphorus (P^{-32}) uptake from soil. Plant Soil 19:147–152

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

Gahoonia TS, Nielsen NE (2004) Barley genotypes with long root hairs sustain high grain yields in low-P field. Plant Soil 262:55–62

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

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

Gardner WK, Barber DA, Parbery DG (1983) The acquisition of phosphorus by *Lupinus albus* L. III. The probable mechanism by which phosphorus movement in the soil-root interface is enhanced. Plant Soil 70:107–124

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 Soil 218:159–171

George TS, Richardson AE (2008) Potential and limitations to improving crops for enhanced phosphorus utilisation. In: White PJ, Hammond JP (eds) The ecophysiology of plant-phosphorus interactions. Plant Ecophysiology, vol. 7. Springer, Dordrecht, pp 247–270

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

George TS, Gregory PJ, Robinson JS, Buresh RJ, Jama B (2002b) Utilisation of soil organic P by agroforestry and crop species in the field, western Kenya. Plant Soil 246:53–63

George TS, Richardson AE, Hadobas PA, Simpson RJ (2004) Characterisation of transgenic *Trifolium subterraneum* L. which expresses *phyA* and releases extracellular phytase:

Growth and phosphorus nutrition in laboratory media and soil. Plant Cell Environ 27:1351–1361

George TS, Richardson AE, Simpson RJ (2005a) Behaviour of plant-derived extracellular phytase upon addition to soil. Soil Biol Biochem 37:977–988

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

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

George TS, Gregory PJ, Simpson RJ, Richardson AE (2007a) Differential interactions of *Aspergillus niger* and *Peniophora lycii* phytases with soil particles affects the hydrolysis of inositol phosphates. Soil Biol Biochem 39:793–803

George TS, Simpson RJ, Hadobas PA, Marshall DJ, Richardson AE (2007b) Accumulation and phosphatase-lability of organic phosphorus in fertilized pasture soils. Aust J Agric Res 58:47–55

George TS, Hocking PJ, Gregory PJ, Richardson AE (2008) Variation of root-associated phosphatase in wheat cultivars explains their ability to utilise organic P substrates in-vitro, but does not effectively predict P-nutrition in a range soils. Environ Exp Bot 64:239–249

George TS, Brown LK, Newton AC, Hallett PD, Sun BH, Thomas WTB, White PJ (2011) Impact of soil tillage on the robustness of the genetic component of variation in phosphorus (P) use efficiency in barley (*Hordeum vulgare* L.). Plant Soil 339:113–123

Gerke J (1992) Phosphate, aluminium and iron in the soil solution of three different soils in relation to varying concentrations of citric acid. Z Pflanz Bodenkunde 155:339–343

Gerke J (1994) Kinetics of soil phosphate desorption as affected by citric acid. Z Pflanz Bodenkunde 157:17–22

Giaveno C, Celi L, Richardson AE, Simpson RJ, Barberis E (2010) Interaction of phytases with soil minerals and availability of substrate affects the hydrolysis of inositol phosphates. Soil Biol Biochem 42:491–498

Gilbert GA, Knight JD, Vance CP, Allan DL (1999) Acid phosphatase activity in phosphorus-deficient white lupin roots. Plant Cell Environ 22:801–810

Glassop D, Smith SE, Smith FW (2005) Cereal phosphate transporters associated with the mycorrhizal pathway of phosphate uptake into roots. Planta 222:688–698

Godwin DC, Wilson EJ (1976) Prospects for selecting plants with increased P efficiency. In: Blair GJ (ed) Reviews in rural science. Ill. The efficiency of phosphorus utilization. University of New England Press, Armidale, pp 131–139

Goos RJ, Johnson BE, Stack RW (1994) *Penicillium bilaji* and phosphorus fertilization effects on the growth, development yield and common root rot severity of spring wheat. Fert Res 39:97–103

Górny AG, Sodkiewicz T (2001) Genetic analysis of the nitrogen and phosphorus utilization efficiencies in mature spring barley plants. Plant Breeding 120:129–132

Grace EJ, Smith FA, Smith SE (2009) Deciphering the arbuscular mycorrhizal pathway of P uptake in non-responsive host plant species. In: Azcón-Aguilar C, Barea JM, Gianinazzi S, Gianinazzi-Pearson (eds) Functional processes and ecological impact. Springer, Heidelberg, pp 89–106

Graham JH, Miller RM (2005) Mycorrhizas: gene to function. Plant Soil 274:79–100

Gruber BD, Ryan PR, Richardson AE, Tyerman SD, Ramesh S, Hebb DM, Howitt SM, Delhaize E (2010) *HvALMT1* from barley is involved in the transport of organic anions. J Exp Bot 61:1455–1467

Gruber BD, Delhaize E, Richardson AE, Roessner U, James RA, Howitt SM, Ryan PR (2011) Characterisation of *HvALMT1* function in transgenic barley plants. Func Plant Biol 38:163–175

Gulden RH, Vessey JK (2000) *Penicillium bilaii* inoculation increases root hair production in field pea. Can J Plant Sci 80:801–804

Guttieri M, Bowen D, Dorsch JA, Raboy V, Souza E (2004) Identification and characterization of a low phytic acid wheat. Crop Sci 44:418–424

Gyaneshwar P, Naresh Kumar G, Parekh LJ, Poole PS (2002) Role of soil microorganisms in improving P nutrition of plants. Plant Soil 245:83–93

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

Harvey PR, Warren RA, Wakelin SA (2009) Potential to improve root access to phosphorus: the role of non-symbiotic microbial inoculants in the rhizosphere. Crop Pasture Sci 60:144–151

Haugland RA, Varma M, Wymer LJ, Vesper SJ (2004) Quantitative PCR analysis of selected *Aspergillus*, *Penicillium* and *Paecilomyces* species. Syst Appl Microbiol 27:198–210

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

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

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

Helyar KR (1998) Efficiency of nutrient utilization and sustaining soil fertility with particular reference to phosphorus. Field Crops Res 56:187–195

Henry A, Chaves NF, Kleinman PJA, Lynch JP (2010a) Will nutrient-efficient genotypes mine the soil? Effects of genetic differences in root architecture in common bean (*Phaseolus vulgaris* L.) on soil phosphorus depletion in a low-input agro-ecosystem in Central America. Field Crops Res 115:67–78

Henry A, Rosas JC, Beaver JS, Lynch JP (2010b) Multiple stress response and below ground competition in multi-

lines of common bean (*Phaseolus vulgaris* L.). Field Crops Res 117:209–218
Hetrick BAD (1991) Mycorrhizas and root architecture. Experientia 47:355–362
Hetrick BAD, Wilson GWT, Todd TC (1996) Mycorrhizal response in wheat cultivars: relationship to phosphorus. Can J Bot 74:19–25
Hill JO, Simpson RJ, Wood JT, Moore AD, Chapman DF (2005) The phosphorus and nitrogen requirements of temperate pasture species and their influence on grassland botanical composition. Aust J Agric Res 56:1027–1039
Ho MD, Rosas JC, Brown KM, Lynch JP (2005) Root architectural tradeoffs for water and phosphorus acquisition. Func Plant Biol 32:737–748
Hocking PJ, Jeffery S (2004) Cluster-root production and organic anion exudation in a group of old-world lupins and a new-world lupin. Plant Soil 258:135–150
Hocking PJ, Keerthisinghe G, Smith FW, Randall PJ (1997) Comparison of the ability of different crop species to access poorly-available soil phosphorus. In: Ando T, Fujita K, Mae T, Matsumoto H, Mori S, Sekiya J (eds) Plant nutrition for sustainable food production and environment. Kluwer Academic Publishers, Dordrecht, pp 305–308
Hocking AD, Whitelaw M, Harden TJ (1998) *Penicillium radicum* sp. nov. from the rhizosphere of Australian wheat. Mycol Res 102:801–806
Horst WJ, Kamh M, Jibrin JM, Chude VO (2001) Agronomic measures for increasing P availability to crops. Plant Soil 237:211–223
Huyghe C (1997) White lupin (*Lupinus albus* L). Field Crops Res 53:147–160
Itoh S, Barber SA (1983) Phosphorus uptake by six plant species as related to root hairs. Agron J 75:457–461
Jakobsen I, Chen BD, Munkvold L, Lundsgaard T, Zhu Y-G (2005a) Contrasting phosphate acquisition of mycorrhizal fungi with that of root hairs using the root hairless barley mutant. Plant Cell Environ 28:928–938
Jakobsen I, Leggett ME, Richardson AE (2005b) Rhizosphere microorganisms and plant phosphorus uptake. In: Sims JT, Sharpley AN (eds) Phosphorus, agriculture and the environment. American Society for Agronomy, Madison, pp 437–494
Javot H, Pumplin N, Harrison MJ (2007) Phosphate in the arbuscular mycorrhizal symbiosis: transport properties and regulatory roles. Plant Cell Environ 30:310–322
Jeschke WD, Pate JS (1995) Mineral nutrition and transport in xylem and phloem of *Banksia prionotes* (Proteaceae), a tree with dimorphic root morphology. J Exp Bot 46:895–905
Johnson NC, Graham JH, Smith FA (1997) Functioning of mycorrhizal associations along the mutualism-parasitism continuum. New Phytol 135:575–585
Jones DL (1998) Organic acids in the rhizosphere—a critical review. Plant Soil 205:25–44
Jones DL, Darrah PR (1994) Role of root-derived organic acids in the mobilisation of nutrients from the rhizosphere. Plant Soil 166:247–257
Jones DL, Dennis PG, Owen AG, van Hees PAW (2003) Organic acid behaviour in soils—misconceptions and knowledge gaps. Plant Soil 248:31–41
Jungk A (2001) Root hairs and the acquisition of plant nutrients from soil. J Plant Nutr Soil Sci 164:121–129
Karamanos RE, Flore NA, Harapiak JT (2010) Re-visiting use of *Penicillium bilaii* with phosphorus fertilization of hard red spring wheat. Can J Plant Sci 90:265–277
Khademi Z, Jones DL, Malakouti MJ, Asadi F, Ardebili M (2009) Organic acid mediated nutrient extraction efficiency in three calcareous soils. Aust J Soil Res 47:213–220
Khademi Z, Jones DL, Malakouti MJ, Asadi F (2010) Organic acids differ in enhancing phosphorus uptake by *Triticum aestivum* L.- effects of rhizosphere concentration and counterion. Plant Soil 334:151–159
Khan SA, Hamayun M, Yoon M, Kim H-Y, Suh S-Y, Hwang S-K, Kim J-M, Lee I-Y, Choo Y-S, Yoon U-H, Kong W-S, Lee B-M, Kim J-G (2008) Plant growth promotion and *Penicillium citrinum*. BMC Microbiol 8:231–40
Khan MS, Zaidi A, Ahemad M, Oves M, Wani PA (2010) Plant growth promotion by phosphate solubilizing fungi—current perspective. Arch Agron Soil Sci 56:73–98
Kirk GJD (1999) A model for phosphate solubilization by organic anion excretion from plant roots. Eur J Soil Sci 50:369–378
Kochian LV, Hoekenga OA, Pineros MA (2004) How do crop plants tolerate acid soils?—Mechanisms of aluminum tolerance and phosphorous efficiency. Ann Rev Plant Biol 55:459–493
Konings H, Verschuren G (1980) Formation of aerenchyma in roots of *Zea mays* in aerated solutions, and its relation to nutrient supply. Physiol Plant 49:265–279
Kothari SK, Marschner H, George E (1990) Effect of VA mycorrhizal fungi and rhizosphere microorganisms on root and shoot morphology, growth and water relations in maize. New Phytol 116:303–311
Kovermann P, Meyer S, Hortensteiner S, Picco C, Scholz-Starke J, Ravera S, Lee Y, Martinoia E (2007) The *Arabidopsis* vacuolar malate channel is a member of the ALMT family. Plant J 52:1169–1180
Koyama H, Takita E, Kawamura A, Hara T, Shibata D (1999) Over expression of mitochondrial citrate synthase gene improves the growth of carrot cells in Al-phosphate medium. Plant Cell Physiol 40:482–488
Koyama H, Kawamura A, Kihara T, Hara T, Takita E, Shibata D (2000) Overexpression of mitochondrial citrate synthase in *Arabidopsis thaliana* improved growth on a phosphorus limited soil. Plant Cell Physiol 41:1030–1037
Kucey RMN (1983) Phosphate-solubilizing bacteria and fungi in various cultivated and virgin Alberta soils. Can J Soil Sci 63:671–678
Kucey RMN (1987) Increased phosphorus uptake by wheat and field beans inoculated with a phosphorus-solubilizing *Penicillium bilaji* strain and with vesicular-arbuscular mycorrhizal fungi. Appl Environ Microbiol 53:2699–2703
Kucey RMN (1988) Effect of *Penicillium bilaji* on solubility and uptake of P and micronutrients from soil by wheat. Can J Soil Sci 68:261–270
Kucey RMN, Leggett ME (1989) Increased yields and phosphorus uptake by Westar canola (*Brassica napus* L.) inoculated with a phosphate-solubilizing isolate of *Penicillium bilaji*. Can J Soil Sci 69:425–432

Kucey RMN, Janzen HH, Leggett ME (1989) Microbially mediated increases in plant-available phosphorus. Adv Agron 42:199–228

Kumar V, Sinha AK, Makkar HPS, Becker K (2010) Dietary roles of phytate and phytase in human nutrition: A review. Food Chem 120:945–959

Lambers H, Poorter H (1992) Inherent variation in growth-rate between higher-plants—a search for physiological causes and ecological consequences. Adv Ecol Res 23:187–261

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

Lambers H, Raven JA, Shaver GR, Smith SE (2008) Plant nutrient-acquisition strategies change with soil age. Trends Ecol Evol 23:95–103

Lambers H, Brundrett MC, Raven JA, Hopper SD (2010) Plant mineral nutrition in ancient landscapes: high plant species diversity on infertile soils is linked to functional diversity for nutritional strategies. Plant Soil 334:11–31

Lambers H, Finnegan PM, Laliberté E, Pearse SJ, Ryan MH, Shane MW, Veneklaas EJ (2011) Phosphorus nutrition of proteaceae in severely phosphorus-impoverished soils: Are there lessons to be learned for future crops? Plant Physiol 156:1058–1066

Lamont B (1973) Factors affecting the distribution of proteoid roots within the root systems of two *Hakea* species. Aust J Bot 21:165–187

Leggett M, Cross J, Hnatowich G, Holloway G (2007) Challenges in commercializing a phosphate-solubilizing microorganisms: *Penicillium bilaiae*, a case history. In: Velázquez E, Rodríguez-Barrueco C, Velázquez E, Rodríguez-Barrueco C (eds) First international meeting on microbial phosphate solubilization. Springer, Dordrecht, pp 215–222

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

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

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

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

Li HY, Smith SE, Holloway RE, Zhu Y-G, Smith FA (2006) Arbuscular mycorrhizal fungi contribute to phosphorus uptake by wheat grown in a phosphorus-fixing soil even in the absence of positive growth responses. New Phytol 172:536–543

Li HY, Smith FA, Dickson S, Holloway RE, Smith SE (2008) Plant growth depressions in arbuscular mycorrhizal symbiosis: not just caused by carbon drain? New Phytol 178:852–862

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

Liao H, Yan X, Rubio G, Beebe SE, Blair MW, Lynch JP (2004) Genetic mapping of basal root gravitropism and phosphorus acquisition efficiency in common bean. Funct Plant Biol 31:959–970

Liao M, Hocking PJ, Dong B, Delhaize E, Richardson AE, Ryan PR (2008) Genotypic variation in phosphorus efficiency among wheat genotypes grown on two contrasting Australian soils. Aust J Agr Res 59:157–166

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

Lung S-C, Lim BL (2006) Assimilation of phytate-phosphours by the extracellualr phytase activity of tobacco (*Nicotiana tabaccum*) is affected by the availabiliyt of souluble phytate. Plant Soil 279:187–199

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

Lynch JP (2007) Roots of the second green revolution. Aust J Bot 55:1–20

Lynch JP, Brown KM (1998) Regulation of root architecture by phosphorus availability. In: Lynch JP, Deikman J (eds) Phosphorus in plant biology: Regulatory roles in molecular, cellular, organismic and ecosystem processes. American Society of Plant Biologists, Rockville, pp 148–156

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

Lynch JP, Brown KM (2006) Whole plant adaptations to low phosphorus availability. In: Huang B (ed) Plant-environment interactions. CRC, Boca Raton, pp 209–242

Lynch JP, Brown KM (2008) Root strategies for phosphorus acquisition. In: White PJ, Hammond JP (eds) The ecophysiology of plant-phosphorus interactions. Plant Ecophysiology, vol. 7. Springer, Dordrecht, pp 83–116

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

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

Lynch JP, Nielsen KL, Davis RD, Jablokow AG (1997) SimRoot: modelling and visualization of root systems. Plant Soil 188:139–151

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

Ma Z, Walk TC, Marcus A, Lynch JP (2001b) Morphological synergism in root hair length, density, initiation and geometry for phosphorus acquisition in *Arabidopsis thaliana*: A modeling approach. Plant Soil 236:221–35

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

Magid J, Tiessen H, Condron LM (1996) Dynamics of organic phosphorus in soils under natural and agricultural ecosystems. In: Piccolo A (ed) Humic substances in terrestrial ecosystems. Elsevier Science, Amsterdam, pp 429–466

Mano Y, Omori F, Takamizo T, Kindiger B, Bird RM, Loaisiga CH, Takahashi H (2007) QTL mapping of root aerenchy-

ma formation in seedlings of a maize x rare teosinte *Zea nicaraguensis* cross. Plant Soil 295:103–113

Manske GGB, Ortiz-Monasterio JI, Van Ginkel M, Gonzalez RM, Rajaram S, Molina E, Vlek PLG (2000) Traits associated with improved P-uptake efficiency in CIMMYT's semidwarf spring bread wheat grown on acid Andisols in Mexico. Plant Soil 221:189–204

Matzek V, Vitousek PM (2009) N:P stoichiometry and protein: RNA ratios in vascular plants: an evaluation of the growth-rate hypothesis. Ecol Lett 12:765–771

McIvor JG, Guppy C, Probert ME (2011) Phosphorus requirements of tropical grazing systems: the northern Australian experience. Plant Soil 349(1–2):55–67

McLaughlin MJ, Fillery IR, Till AR (1992) Operation of the phosphorus, sulphur and nitrogen cycles. In: Australia's renewable resources: sustainability and global change. Bureau Rural Res Proc 14:67–116

McLaughlin MJ, McBeath TM, Smernik R, Stacey SP, Ajiboye B. Guppy, C (2011) The chemical nature of P accumulation in agricultural soils—implications for fertiliser management and design: an Australian perspective. Plant Soil 349(1–2):69–87

Miguel MA (2004) Genotypic variation in root hairs and phosphorus efficiency in common bean (*Phaseolus vulgaris* L.). MS thesis. Pennsylvania State University, University Park

Miguel MA (2011) Functional role and synergistic effect of root traits for phosphorus acquisition efficiency and their genetic basis in common bean (*Phaseolus vulgaris* L.). PhD thesis. Pennsylvania State University, University Park

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. Func Plant Biol 30:973–985

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

Morrow de la Riva L (2010) Root etiolation as a strategy for phosphorus acquisition in common bean, MS thesis. Pennsylvania State University, University Park

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

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

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

Nuruzzaman M, Lambers H, Bolland MDA, Veneklaas EJ (2005) Phosphorus benefits of different legume crops to subsequent wheat grown in different soils of Western Australia. Plant Soil 271:175–187

Nye PH (1973) The relation between the radius of a root and its nutrient absorbing power. J Exp Bot 24:783–786

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

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

Oburger E, Kirk GJD, Wenzel WW, Puschenreiter M, Jones DL (2009) Interactive effects of organic acids in the rhizosphere. Soil Biol Biochem 41:449–457

Oburger E, Jones DL, Wenzel WW (2011) Phosphorus saturation and pH differentially regualte the efficiency of organcic acid anion-mediated P solubilization mechanims in soil. Plant Soil 341:363–382

Ochoa IE, Blair MW, Lynch JP (2006) QTL Analysis of adventitious root formation in common bean (*Phaseolus vulgaris* L.) under contrasting phosphorus availability. Crop Sci 46:1609–1621

Osorio NW, Habte M (2001) Synergistic influence of an arbuscular mycorrhizal fungus and a P solubilizing fungus on growth and P uptake of *Leucaena leucocephala* in an oxisol. Arid Land Res Manage 15:263–274

Ozanne PG (1980) Phosphate nutrition of plants—a general treatise. In: Khasawneh FE, Sample EC, Kamprath EJ (eds) The role of phosphorus in agriculture. American Society of Agronomy, Madison, pp 559–616

Ozturk L, Eker S, Torun B, Cakmak I (2005) Variation in phosphorus efficiency among 73 bread and durum wheat genotypes grown in a phosphorus-deficient calcareous soil. Plant Soil 269:69–80

Pang J, Ryan MH, Tibbett M, Cawthray GR, Siddique KHM, Bolland MDA, Denton MD, Lambers H (2010) Variation in morphological and physiological parameters in herbaceous perennial legumes in response to phosphorus supply. Plant Soil 331:241–255

Pate JS, Verboom WH, Galloway PD (2001) Co-occurrence of *Proteaceae*, laterite and related oligotrophic soils: coincidental associations or causative inter-relationships? Aust J Bot 49:529–560

Pearse SJ, Veneklaas EJ, Cawthray GR, Bolland MDA, Lambers H (2006) Carboxylate release of wheat, canola and 11 grain legume species as affected by phosphorus status. Plant Soil 288:127–139

Pearse SJ, Veneklaas EJ, Cawthray GR, Bolland MDA, Lambers H (2007) Carboxylate composition of root exudates does not relate consistently to a crop species' ability to use phosphorus from aluminium, iron or calcium phosphate sources. New Phytol 173:181–190

Peix A, Rivas-Boyero AA, Mateos PF, Rodriguez-Barrueco C, Martínez-Molina E, Velazquez E (2001) Growth promotion of chickpea and barley by a phosphate solubiliizing strain of *Mesorhizobium mediterraneum* under growth chamber conditions. Soil Biol Biochem 33:103–110

Perry RP (2007) Balanced production of ribosomal proteins. Gene 401:1–3

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

Pinkerton A, Smith FW, Lewis DC (1997) Pasture species. In: Reuter DJ, Robinson JB (eds) Plant analysis: An interpretation manual. CSIRO Publishing, Collingwood, pp 287–346

Polglase PJ, Attiwill PM, Adams MA (1992) Nitrogen and phosphorus cycling in relation to standage of *Eucalyptus*

regans F.Muell. 3. Labile inorganic and organic P, phosphatase-activity and P-availability. Plant Soil 142:177–185

Postma JA, Lynch JP (2011) Theoretical evidence for the functional benefit of root cortical aerenchyma in soils with low phosphorus availability. Ann Bot 107:829–841

Raboy V (2003) *myo*-Inositol-1,2,3,4,5,6-hexakisphosphate. Phytochem 64:1033–1043

Raboy V (2009) Approaches and challenges to engineering seed phytate and total phosphorus. Plant Sci 177:281–296

Rao IM, Terry N (1989) Leaf phosphate status, photosynthesis, and carbon partitioning in sugar beet: I. Changes in growth, gas exchange, and Calvin cycle enzymes. Plant Physiol 90:814–819

Rasmussen SK, Ingvardsen CR, Torp AM (2010) Mutations in genes controlling the biosynthesis and accumulation of inositol phosphates in seeds. Biochem Soc Trans 38:689–694

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

Reddell P, Yun Y, Shipton WA (1997) Cluster roots and mycorrhizae in *Casuarina cunninghamiana*: Their occurrence and formation in relation to phosphorus supply. Aust J Bot 45:41–51

Relwani L, Krishna P, Reddy MS (2008) Effect of carbon and nitrogen sources on phosphate solubilisation by a wild-type strain and UV-induced mutants of *Aspergillus tubigensis*. Curr Microbiol 57:401–406

Rice WA, Lupwayi NZ, Olsen PE, Schlechte D, Gleddie SC (2000) Field evaluation of dual inoculation of alfalfa with *Sinorhizobium meliloti* and *Penicillium bilaii*. Can J Plant Sci 80:303–308

Richardson AE (1994) Soil microorganisms and phosphorus availablility. In: Pankhurst CE, Doube BM, Gupta VVSR, Grace PR (eds) Management of the soil biota in sustainable farming systems. CSIRO Publishing, Collingwood, pp 50–62

Richardson AE, Hadobas PA (1997) Soil isolates of *Pseudomonas* spp. that utilise inositol phosphates. Can J Microbiol 43:509–516

Richardson AE, Simpson RJ (2011) Soil microorganisms mediating phosphorus availability. Plant Physiol 156:989–996

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

Richardson AE, Hadobas PA, Hayes JE, O'Hara CP, Simpson RJ (2001b) Utilization of phosphorus by pasture plants supplied with *myo*-inositol hexaphosphate is enhanced by the presence of soil microorganisms. Plant Soil 229:47–56

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

Richardson AE, George TS, Jackobsen I, Simpson RJ (2007) Plant access to inositol phosphates in soil. In: Turner BL, Richardson AE, Mullaney EJ (eds) Inositol phosphates: Linking agriculture and the environment. CABI Publishing, Wallingford, pp 242–260

Richardson AE, Barea JM, McNeill AM, Prigent-Combaret C (2009a) Acquisition of phosphorus and nitrogen in the rhizosphere and plant growth promotion by microorganisms. Plant Soil 321:305–339

Richardson AE, Hocking PJ, Simpson RJ, George TS (2009b) Plant mechanisms to optimise access to soil phosphorus. Crop Pasture Sci 60:124–143

Robinson D (2005) Integrated root responses to variations in nutrient supply. In: BassiriRad H (ed) Nutrient acquisition by plants: an ecological perspective. Springer, Berlin, pp 43–62

Robson AD, Abbott LK, Malajczuk N (1994) Management of mycorrhizas in agriculture, horticulture and forestry. Developments in Plant and Soil Sciences, Vol. 56. Kluwer Academic Publishers

Rodríguez H, Fraga R, Gonzalez T, Bashan Y (2006) Genetics of phosphate solubilisation and its potential applications for improving plant growth-promoting bacteria. Plant Soil 287:15–21

Roelofs RFR, Rengel Z, Cawthray GR, Dixon KW, Lambers H (2001) Exudation of carboxylates in Australian Proteaceae: chemical composition. Plant Cell Environ 24:891–903

Rose TJ, Rengel Z, Qn M, Bowden JW (2007) Differential accumulation patterns of phosphorus and potassium by canola cultivars compared to wheat. Z Pflanz Bodenkunde 170:404–411

Rose TJ, Pariasca-Tanaka J, Rose MT, Fukuta Y, Wissuwa M (2010) Genotypic variation in grain phosphorus concentration, and opportunities to improve P-use efficiency in rice. Field Crops Res 119:154–160

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

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

Ryan MH, Angus JF (2003) Arbuscular mycorrhizae in wheat and field pea crops on a low P soil: increased Zn-uptake but no increase in P-uptake or yield. Plant Soil 250:225–239

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

Ryan MH, Small DR, Ash JE (2000) Phosphorus controls the level of colonisation by arbuscular mycorrhizal fungi in conventional and biodynamic irrigated dairy pastures. Aust J Exp Agric 40:663–670

Ryan MH, McInerney JK, Record IR, Angus JF (2008) Zinc bioavailability in wheat grain in relation to phosphorus fertiliser, crop sequence and mycorrhizal fungi. J Sci Food Agric 88:1208–1216

Ryan MH, van Herwaarden AF, Angus JF, Kirkegaard JA (2005) Reduced growth of autumn-sown wheat in a low-P soil is associated with high colonisation by arbuscular mycorrhizal fungi. Plant Soil 270:275–286

Ryan PR, Delhaize E (2010) The convergent evolution of aluminium resistance in plants exploits a convenient currency. Func Plant Biol 37:275–284

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

Ryan PR, Delhaize E, Randall PJ (1995) Characterisation of Al-stimulated efflux of malate from the apices of Al-tolerant wheat roots. Planta 196:103–111

Sampson RA, Seifert KA, Kuijpers AFA, Houbraken JAMP, Frisvad JC (2004) Phylogenetic analyses of *Penicillium* subgenus *Penicillium*, using partial using partial β-tubulin sequences. Stud Mycol 49:175–200

Sánchez PA (2010) Tripling crop yields in tropical Africa. Nature Geosci 3:299–300

Santonoceto C, Hocking PJ, Braschkat J, Randall PJ (2002) Mineral nutrient uptake and removal by canola, Indian mustard, and Linola in two contrasting environments, and implications for carbon cycle effects on soil acidification. Aust J Agric Res 53:459–470

Sas L, Rengel Z, Tang C (2001) Excess cation uptake, and extrusion of protons and organic acid anions by *Lupinus albus* under phosphorus deficiency. Plant Sci 160:1191–1198

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

Sasaki T, Mori IC, Furuichi T, Munemasa S, Toyooka K, Matsuoka K, Murata Y, Yamamoto Y (2010) Closing plant stomata requires a homolog of an Aluminum-activated malate transporter. Plant Cell Physiol 51:354–365

Savard ME, Miller JD, Blais LA, Seifert KA, Sampson RA (1994) Secondary metabolites of *Penicillium bilaii* strain PB-50. Mycopathologica 127:19–27

Schweiger PF, Jakobsen I (1999) Direct measurement of arbuscular mycorrhizal phosphorus uptake into field-grown winter wheat. Agron J 91:998–1002

Schweiger PF, Robson AD, Barrow NJ (1995) Root hair length determines beneficial effect of a Glomus species on shoot growth of some pasture species. New Phvtol 131:247–254

Seifert KA, Sampson RA, de Waard JR, Houbraken J, Levesque AC, Moncalvo J-M, Louis-Selze G, Hebet PDM (2007) Prospects for fungus identification using *CO1* DNA barcodes, with *Penicillium* as a test case. Proc Nat Acad Sci USA 104:3901–3906

Sekiya N, Yano K (2010) Seed P-enrichment as an effective P supply to wheat. Plant Soil 327:347–354

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

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

Shane MW, De Vos M, De Roock S, Cawthray GR, Lambers H (2003a) Effect of external phosphorus supply on internal phosphorus concentration and the initiation, growth and exudation of cluster roots in *Hakea prostrata* R.Br. Plant Soil 248:209–219

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

Shane MW, Dixon KW, Lambers H (2005) The occurrence of dauciform roots amongst Western Australian reeds, rushes and sedges, and the impact of phosphorus supply on dauciform-root development in *Schoenus unispiculatus* (Cyperaceae). New Phytol 165:887–898

Shane MW, Cawthray GR, Cramer MD, Kuo J, Lambers H (2006) Specialized 'dauciform' roots of Cyperaceae are structurally distinct, but functionally analogous with 'cluster' roots. Plant Cell Environ 29:1989–1999

Shang C, Stewart JWB, Huang PM (1992) pH effect on kinetics of adsorption of organic and inorganic phophates by short-range ordered aluminium and iron precipitates. Geoderma 53:1–14

Shu LZ, Shen JB, Rengel Z, Tang CX, Zhang FS (2007a) Cluster root formation by *Lupinus albus* is modified by stratified application of phosphorus in a split-root system. J Plant Nutr 30:1–3

Shu LZ, Shen JB, Rengel Z, Tang CX, Zhang FS, Cawthray GR (2007b) Formation of cluster roots and citrate exudation by *Lupinus albus* in response to localized application of different phosphorus sources. Plant Sci 172:1017–1024

Silberbush M, Barber SA (1983) Sensitivity of simulated phosphorus uptake to parameters used by a mechanistic-mathematical model. Plant Soil 74:93–100

Simpson RJ, Oberson A, Culvenor RA, Ryan MH, Veneklaas EJ, Lambers H, Lynch JP, Ryan PR, Delhaize E, Smith FA, Smith SE, Harvey PR, Richardson AE (2011) Strategies and agronomic interventions to improve the phosphorus-use efficiency of farming systems. Plant Soil 349(1–2):89–120

Singh SP, Urrea CA, Gutiérrez JA, Garcia J (1989) Selection for yield at two fertilizer levels in small-seeded common bean. Can J Plant Sci 69:1011–1017

Skene KR (1998) Cluster roots: some ecological considerations. J Ecol 86:1062–1066

Smernik RJ, Dougherty WJ (2007) Identification of phytate in phosphorus-31 nuclear magnetic resonance spectra: The need for spiking. Soil Sci Soc Am J 71:1045–1050

Smith SE, Read DJ (2008) Mycorrhizal Symbiosis. Academic, London

Smith SE, Smith FA (2011) Roles of arbuscular mycorrhizas in plant nutrition and growth: new paradigms from cellular to ecosystem scales. Ann Rev Plant Biol 62:227–250

Smith SE, Jakobsen I, Grønlund M, Smith FA (2011) Roles of arbuscular mycorrhizas in plant phosphorus nutrition: Interactions between pathways of phosphorus uptake in arbuscular mycorrhizal roots have important implications for understanding and manipulating plant phosphorus acquisition. Plant Physiol 156:1050–1057

Ström L, Owen AG, Godbold DL, Jones DL (2002) Organic acid mediated mobilization in the rhizosphere and uptake by maize. Soil Biol Biochem 34:703–710

Syers JK, Johnston AE, Curtin D (2008). Efficiency of soil and fertilizer phosphorus use—reconciling changing concepts of soil phosphorus behaviour with agronomic information. FAO Fertilizer and Plant Nutrition Bulletin 18. FAO, United Nations, Rome

Tadano T, Ozawa K, Sakai H, Osaki M, Matsui H (1993) Secretion of acid phosphatase be the roots of crop plants under phosphorus-deficient conditions and some properties of the enzyme secreted by lupin roots. Plant Soil 155(156):95–98

Takeda M, Knight JD (2006) Enhanced solubilisation of rock phosphate by *Penicillium bilaiae* in pH-buffered solution culture. Can J Microbiol 52:1121–1129

Tang J, Leung A, Leung C, Lim BL (2006) Hydrolyis of precipiatated phytate by three distinct families of phytases. Soil Biol Biochem 38:1316–1324

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

Tarafdar JC, Jungk A (1987) Phosphatase activity in the rhizosphere and its relation to the depletion of soil organic phosphorus. Biol Fert Soils 3:199–204

Taurian T, Anzuay MS, Angelini JG, Tonelli ML, Luduena L, Pena D, Ibanez F, Fabra A (2010) Phosphate-solubilizing peanut associated bacteria: screening for plant growth-promoting activities. Plant Soil 329:421–431

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 aluminium. Plant Physiol 127:1836–1844

Thompson JP (1987) Decline of vesicular-arbuscular mycorrhizae in long fallow disorder of field crops and its expression in phosphorus deficiency of sunflower. Aust J Agric Res 38:847–867

Thompson JP (1991) Improving the mycorrhizal condition of the soil through cultural practices and effects on growth and phosphorus uptake in plants. In: Johansen C, Lee KK, Sahrawat KL (eds) Phosphorus nutrition of grain legumes in the semi-arid tropics. ICRISAT, Hyderabad, Andra Pradesh, pp 117–137

Thomson CJ, Bolger TP (1993) Effects of seed phosphorus concentration on the emergence and growth of subterranean clover (*Trifolium subterraneum*). Plant Soil 155 (156):285–288

Thomson BD, Robson AD, Abbott LK (1986) Effects of phosphorus on the formation of mycorrhizas by Gigaspora calospora and Glomus fasciculatum in relation to root carbohydrates. New Phytol 103:751–765

Trachsel S, Kaeppler SM, Brown KM, Lynch JP (2011) Shovelomics: high throughput phenotyping of maize (*Zea mays* L.) root architecture in the field. Plant Soil 341:75–87

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

Turner BL, Papházy MJ, Haygarth PM, McKelvie ID (2002) Inositol phosphates in the environment. Philos T Roy Soc B 357:449–469

Tye AJ, Siu KY, Leung YC, Lim BL (2002) Molecular cloning and the biochemical characterisation of two novel phytases from *B. subtilis* 168 and *B. licheniformis*. Appl Microbiol Biotechnol 59:190–197

Unno Y, Okubo K, Wasaki J, Shinano T, Osaki M (2005) Plant growth promotion abilities and microscale bacterial dynamics in the rhizosphere of Lupin analysed by phytate utilization ability. Environ Microbiol 7:396–404

Van den Berg MA, Albang R, Albermann K, Badger JH, Daran JM, Driessen AJ, Garcia-Estrada C, Fedorova ND, Harris DM, Heijne WH, Joardar V, Kiel JA, Kovalchuk A, Martin JF, Nierman WC, Nijland JG, Pronk JT, Roubos JA, van der Klei IJ, van Peij NN, Veenhuis M, von Dohren H, Wagner C, Wortman J, Bovenberg RA (2008) Genome sequencing and analysis of the filamentous fungus *Penicillium chrysogenum*. Nature Biotech 26:1161–1168

Van Kauwenbergh SJ (2010) World phosphate rock reserves and resources. International Fertilizer Development Center, Muscle Shoals

Van Veen JA, Leonard S, van Overbeek LS, Van Elsas JD (1997) Fate and activity of micro-organisms introduced into soil. Microbiol Mol Biol Rev 61:121–135

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

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

Vessey JK, Heisinger KG (2001) Effect of *Penicillium bilaii* inoculation and phosphorus fertilisation on root and shoot parameters of field-grown pea. Can J Plant Sci 81:361–366

Vesterager JM, Nielsen NE, Høgh-Jensen H (2006) Variation in phosphorus uptake and use efficiencies between pigeonpea genotypes and cowpea. J Plant Nutr 29:1869–1888

Wakelin SA, Warren RA, Harvey PR, Ryder MH (2004) Phosphate solubilization by *Penicillium* spp. closely associated with wheat roots. Biol Fert Soils 40:36–43

Wakelin SA, Gupta VVSR, Harvey PR, Ryder MH (2007) The effect of *Penicillium* fungi on plant growth and P mobilisation in neutral to alkaline soils from southern Australia. Can J Microbiol 53:106–115

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

Wang LD, Liao H, Yan XL, Zhuang BC, Dong YS (2004) Genetic variability for root hair traits as related to phosphorus status in soybean. Plant Soil 261:77–84

Wang X, Wang Y, Tian J, Lim BL, Yan X, Liao H (2009) Overexpressing *AtPAP15* enhances phosphorus efficiency in soybean. Plant Physiol 151:233–240

Warner JR, Vilardell J, Sohn JH (2001) Economics of ribosome biosynthesis. Cold Spring Harbor Symposia on Quantitative Biology 66:567–574

Wasaki J, Maruyama H, Tanaka M, Yamamura T, Dateki H, Shinano T, Ito S, Osaki M (2009) Overexpression of the *LaSAP2* gene for secretory acid phosphatase in white lupin improves the phosphorus uptake and growth of tobacco plants. Soil Sci Plant Nutr 55:107–113

Watt RG, Dykes J, Sheiham A (2001) Socio-economic determinants of selected dietary indicators in British preschool children. Public Health Nutr 4:1229–1233

Weaver DM, Wong MTF (2011) Phosphorus balance efficiency and P status in crop and pasture soils with contrasting P buffer indices: scope for improvement. Plant Soil (Special Issue S43—Phosphorus; submitted)

Wei LL, Chen CR, Xu ZH (2010) Citric acid enhances the mobilization of organic phosphorus in subtropical and tropical forest soils. Biol Fert Soils 46:765–769

Weisskopf L, Abou-Mansour E, Fromin N, Tomasi N, Santelia D, Edelkott I, Neumann G, Aragno M, Tabacchi R,

Martinoia E (2006) White lupin has developed a complex strategy to limit microbial degradation of exuded citrate required for phosphate acquisition. Plant Cell Environ 29:919–927, wheat under drought conditions in South Australia. Aust J Exp Agric 39:721–732

Wherrett T, Ryan PR, Delhaize E, Shabala S (2005) Effect of aluminium on membrane potential and ion fluxes at the apices of wheat roots. Func Plant Biol 32:199–208

Whitelaw MA (2000) Growth promotion of plants inoculated with phosphate-solubilizing fungi. Adv Agron 69:99–151

Whitelaw MA, Harden TJ, Bender GL (1997) Plant growth promotion of wheat inoculated with *Penicillium radicum* sp. nov. Aust J Soil Res 35:291–300

Whitelaw MA, Harden TJ, Helyar KR (1999) Phosphate solubilisation in solution culture by the soil fungus *Penicillium radicum*. Soil Biol Biochem 31:655–665

World Bank (2004) World development indicators. The World Bank, Washington

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

Xu JP (2006) Microbial ecology in the age of genomics and metagenomics: concepts, tools and recent advances. Mol Ecol 15:1713–1731

Yadav RS, Tarafdar JC (2003) Phytase and phosphatase producing fungi in arid and semi-arid soils and their efficiency in hydrolyzing different organic P compounds. Soil Biol Biochem 35:745–751

Yan F, Zhu YY, Müller C, Zörb C, Schubert S (2002) Adaptation of H^+-pumping and plasma membrane H^+ ATPase activity in proteoid roots of white lupin under phosphorus deficiency. Plant Physiol 129:50–63

Yan XL, Liao H, Beebe SE, Blair MW, Lynch JM (2004) QTL mapping of root hair and acid exudation traits and their relationship to phosphorus uptake in common bean. Plant Soil 265:17–29

Yao Q, Li XL, Feng G, Christie P (2001) Mobilization of sparingly soluble inorganic phosphates by the external mycelium of an abuscular mycorrhizal fungus. Plant Soil 230:279–285

Yokosho K, Yamaji N, Ueno D, Mitani N, Ma JF (2009) *OsFRDL1* Is a citrate transporter required for efficient translocation of iron in rice. Plant Physiol 149:297–305

Yuen K-Y, Pascal G, Wong SSY, Glaser P, Woo PCY, Kunst F, Cai JJ, Cheung EYL, Médigue C, Danchin A (2003) Exploring the *Penicillium marneffei* genome. Arch Microbiol 179:339–353

Zhu JM, Lynch JP (2004) The contribution of lateral rooting to phosphorus acquisition efficiency in maize (*Zea mays* L.) seedlings. Func Plant Biol 31:949–958

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

Zhu JM, Kaeppler SM, Lynch JP (2005b) Mapping of QTL for lateral root branching and length in maize (*Zea mays* L.) under differential phosphorus supply. Theor Appl Genet 111:688–695

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

Zhu YY, Yan F, Zörb C, Schubert S (2005d) A link between citrate and proton release by proteoid roots of white lupin (*Lupinus albus* L.) grown under phosphorus-deficient conditions. Plant Cell Physiol 46:892–901

Zhu JM, Zhang CC, Lynch JP (2010a) The utility of phenotypic plasticity for root hair length for phosphorus acquisition. Func Plant Biol 37:313–322

Zhu JM, Brown KM, Lynch JP (2010b) Root cortical aerenchyma improves the drought tolerance of maize (*Zea mays* L.). Plant Cell Environ 33:740–749

Zinn KE, Liu J, Allan DL, Vance CP (2009) White lupin (*Lupinus albus*) response to phosphorus stress: evidence for complex regulation of *LaSA*P1. Plant Soil 322:1–15

Zubaidi A, McDonald GK, Hollamby GJ (1999) Nutrient uptake and distribution by bread and durum wheat under drought conditions in South Australia. Aust J Exp Agric 39:721–732