

Efficient use of phosphorus in temperate grassland systems

Richard J Simpson^A, Alan E Richardson^A, Shirley N Nichols^B and James R Crush^B

^A CSIRO Sustainable Agriculture Flagship / CSIRO Plant Industry, GPO Box 1600, Canberra ACT 2601, Australia.

^B AgResearch, Ruakura Research Centre, Private Bag 3123, Hamilton 3240, New Zealand

Contact email: richard.simpson@csiro.au

Abstract. Phosphorus (P) fertilisers are important for high production in many grassland systems. However, there are increasing environmental, economic and strategic issues associated with using P, which is a non-renewable and “effectively finite” global resource. We review the P balance of temperate pastures to identify the factors that contribute to inefficient P use and discuss ways to improve P use efficiency. The most immediate gains can be made by ensuring that pastures are not over-fertilised. Plants with low critical P requirements, particularly as a result of better root foraging, will be important. Root traits such as fine roots (root diameter), branching, length and root hairs, and mycorrhizal associations all contribute to improved root foraging; some are amenable to plant breeding. Plants that can “mine” sparingly-available P in soils by producing organic anions and phosphatases are also needed; as are innovations in fertiliser technology. Soil microorganisms play a crucial role in P acquisition by pastures but are not particularly amenable to management. Selection of pasture species for root characteristics offers a more realistic approach to improving P efficiency but progress, to date, has been minimal. Traditional plant breeding, augmented by marker assisted selection and interspecific hybridisation, are likely to be necessary for progress. Inevitably, P efficient pastures will be achieved most effectively by a combination of plant genetic, fertiliser innovation and management responses. Success will bring economic and environmental benefits from reduced P fertiliser use, with consequent benefits for global resource and food security.

Keywords: Phosphorus use efficiency, phosphorus balance/surplus, root foraging, phosphorus mining, fertilisers

Introduction

Phosphorus (P) fertilisers are now essential for supporting the present and future human population of the world. Currently, about 18 Tg of P per annum is used globally as fertiliser (Cordell and White 2011), with considerable disparity in usage across continents and between different agricultural systems. Additional P inputs to agriculture in the form of manure are probably about 8–17 Tg P/year (estimates vary considerably: Cordell *et al.* 2009; Bouwman *et al.* 2011).

Global rock phosphate “reserves” (high quality deposits) and P “resources” (phosphate rock deposits of lower quality or harder to access; not currently economic to mine) are extensive (van Kauwenburgh 2010). Although there is continuing debate about when the availability of P from global reserves will “peak” (Cordell and White 2011), a recent re-assessment of global P reserves indicates that they may be sufficient to meet global needs for up to 300–400 years at current rates of use (van Kauwenburgh 2010). Irrespective of this debate there are many reasons why it is important that P is used as effectively and efficiently as possible:

- High-quality phosphate rock reserves are non-renewable and, effectively, a finite resource.
- Access to high quality and affordable sources of P is critical for global food security. Presently, the underlying cost of P fertilisers is rising and has more than

doubled since 2000, and the world’s lower-grade P resources will be even more costly to extract.

- P fertiliser is a significant cost for many grazing farms in developed economies and it is often not affordable for smallholder farmers in P deficient areas of the developing world (*e.g.* sub Saharan Africa).
- P use in agriculture is often associated with P loss to the wider environment; even small losses of P to waterways can cause substantial environmental problems.

P balance of grassland farming systems

Under ideal circumstances, P inputs to agriculture would equal P outputs in products (*i.e.* no P surplus; phosphorus balance efficiency [PBE] = P output/P input = 100%). Examples of highly efficient use of P include wheat production on soil with a long history of fertiliser use (United Kingdom), PBE = 90% (Johnston and Syers 2009); extensive cattle production with P supplementation (Australia), PBE = ~100% (McIvor *et al.* 2011). However, high apparent PBE can also be achieved by using relatively poor practices. For example, farms on low P soils that use minimal or no P fertiliser and have relatively low production will achieve a high PBE. PBE may even exceed 100% for very low input farms, indicating unsustainable mining of soil P resources (Burkitt *et al.* 2007).

When P fertilisers are being used in productive agriculture, it is more common that significant P surpluses

are observed (*e.g.* Bouwman *et al.* 2009; Weaver and Wong 2011). For example, in farming systems in Australia, PBE's reported by Weaver and Wong (2011) reflect significant P surpluses (*i.e.* median PBE = 48% for cropping, 29% for dairy, 11-19% for sheep/beef grazing). The ranges in PBE for every enterprise type, however, were very large and reflect a wide range in production goals, fertiliser and management practices. P surpluses in grazing systems are a consequence of either: unavoidable P accumulation in high P-sorbing soils and/or in animal camps; unnecessary accumulations of P in fields due to over-application of P fertiliser and manure; and/or because P is being lost from fields by soil erosion, runoff or leaching.

P accumulation in soil under pasture production

Building soil P fertility: Agricultural soils that are P deficient and cannot, as a consequence, support optimum production are often improved by applying P fertiliser and/or manure at rates that purposefully exceed the rates of P removal and loss so that P accumulates in the soil. P cycling is increased and the plant-available P concentration of the soil is increased to support faster plant growth. Ideally, the build up in soil fertility should not exceed the "critical P requirement" of a pasture. This is typically defined as the plant-available P concentration of soil that corresponds with 90% or 95% of maximum pasture growth.

Excessive applications of P: If P fertiliser continues to be applied at a rate that allows P to accumulate in the grazing system, the critical available P concentration of the topsoil will eventually be exceeded and fertiliser is then being applied in excess of its need. P is often applied in excess of requirements as a result of ignorance of the critical P concentration that is appropriate for a soil-crop system, but over application can also be a consequence of deliberate but poor agronomic practice. In some developed economies it can be the consequence of logistics and disposal problems that occur when animal production facilities in an area generate more manure than the surrounding land can accept for good agronomic practice (Smit *et al.* 2009).

Accumulation of P in soil in "sparingly-available" forms: Even when soil P fertility is being managed adequately, soils that have a moderate to high P-sorption capacity are a net sink for some of the P that is applied. Here we use the term "P sorption" to represent the net process of phosphate movement from soil solution to the solid phase of the soil and ultimately into sparingly-available forms of phosphate as proposed by Barrow (1999) (Fig. 1). The chemistry of sorption reactions in soil is complex and is described elsewhere in more detail (*e.g.* Sample *et al.* 1980; McLaughlin *et al.* 2011). The net rate of phosphate sorption in non-calcareous soils is determined by the sorption capacity of the soil, and is proportional to the concentration of P in soil solution and the time over which phosphate is in contact with the soil. In calcareous soils, the drivers are initially similar but precipitation of calcium phosphates quickly decreases the phosphate concentration of the soil solution to levels that are determined by the solubility product (Barrow 1980).

P also accumulates in slowly-cycling soil organic compounds with the amount of accumulated organic P often being similar to that of sparingly-available phosphate

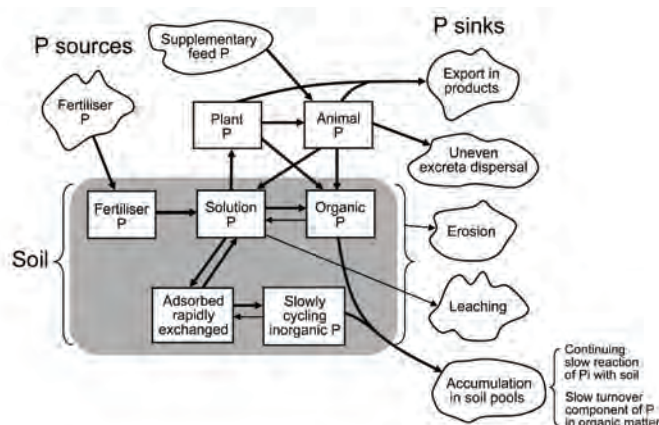


Figure 1. Schematic overview of the P cycle and the sources and net sinks for P in a grazing system (from Simpson *et al.* 2011).

(Helyar *et al.* 1997; George *et al.* 2007). Various components of soil organic matter are mineralised at different rates depending on their chemical and physical protection (Krull *et al.* 2003). Even very resistant materials (such as humus) are mineralised albeit very slowly, so accumulated forms of organic P are also not "fixed". There are some organic P compounds that are recognised components of accumulated organic P (*e.g.* phytate, Turner *et al.* 2002), however, there is also a large component (up to 50%) of high molecular weight organic P material that is associated with stabilised soil organic matter and remains poorly characterised.

The annual rate of P accumulation in grazed fields (*i.e.* the sum of phosphate and organic P accumulations in the soil and in animal camps) has been shown to be positively correlated with the concentration of plant-available P at which the fields were being managed (Fig. 2). This indicates that managing soil fertility at the lowest available P concentration that can deliver high production, or developing pastures that can yield well at lower plant-available soil P concentrations, should also lead to lower rates of P accumulation and reductions in the P surplus of fertilised pasture systems.

P budgets for grazing systems (*e.g.* Lewis *et al.* 1987; McCaskill and Cayley 2000; Simpson *et al.* 2010; Nguyen and Goh 1992) help identify the factors that contribute to inefficient use of P inputs. This is especially the case for budgets of P balance in systems where the plant-available P concentration of the soil has been maintained at a stable level because P accumulations in soil are not then due to an increase in soil P fertility (*i.e.* available P) or excessive fertiliser use:

$$P_{\text{fertiliser}} = P_{\text{export}} + P_{\text{erosion/leaching}} + P_{\text{excreta dispersal}} + P_{\text{soil accum}} + \dots \text{ (Eqn 1)}$$

where: P_{export} = removal of P in products; $P_{\text{erosion/leaching}}$ = P lost by leaching, runoff or soil movement; $P_{\text{excreta dispersal}}$ = P accumulated in small areas of farms as a result of uneven dispersal of animal excreta rendering the P less available; $P_{\text{soil accum}}$ = P accumulating as sparingly-available phosphate or organic P compounds that are slowly mineralised. If the plant-available P concentration of the soil is being maintained at a stable level then: $P_{\text{fertiliser}}$ = the "maintenance" fertiliser requirement.

It becomes clear that P-sorption capacity of a soil is a

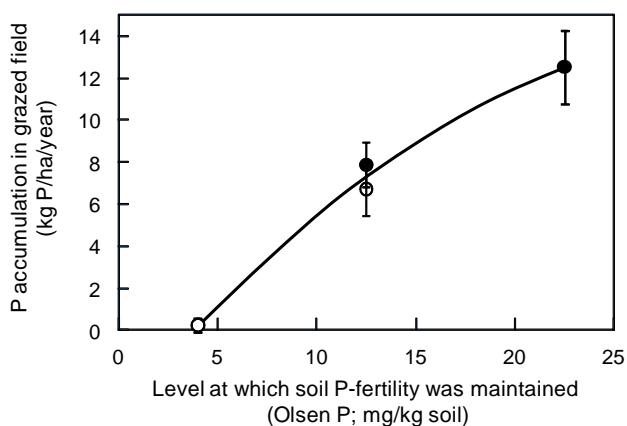


Figure 2. Average annual rates of P accumulation in fields based on acid soil with a moderate P-sorption capacity (Phosphorus Buffering Index = 50, Burkitt *et al.* 2002) that were grazed continuously by 9 sheep/ha (open circles) or 18 sheep/ha (closed circles) and maintained at three levels of plant-available P in the topsoil (0-10 cm depth) over 6 years (from Simpson *et al.* 2010). Soil fertility levels are the midpoint soil test value of the target range for soil fertility management. The expected critical Olsen P concentration for near-maximum pasture growth in this system was 15 mg P/kg. Bars represent 2x standard error.

key variable influencing PBE. This in turn influences the routes by which the P efficiency may be improved. Accumulation of P in soil is a relatively small term in soils with low P-sorption capacity, but P loss by leaching in such soils may be large. The reverse will be true in soils with moderate to high P-sorption capacity and P accumulation in soil will then need to be the main of focus for PBE improvement using agronomic and plant breeding options.

Uneven distribution of excreta in grazed fields

P also accumulates in animal camp areas of grazed fields, and in particular areas of a grazing farm system as a consequence of uneven distribution of animal excreta. Estimates of the relative size of this accumulation term for grazed fields are typically about 5% of the amount of P applied as fertiliser (*e.g.* Metherell 1994) but can be higher in some circumstances [*e.g.* stock camps in steep New Zealand hill pastures (Gillingham *et al.* 1980)].

P loss from grazed fields to the wider environment

P loss due to erosion and runoff is usually a relatively small component of the P balance of a farming system when appropriately managed. Annual losses from grazed and fertilised fields are typically in the range 0.1-3 kg P/ha/year and most often are <1 kg P/ha/year (*e.g.* Monaghan *et al.* 2007). However, there are positive relationships between the concentrations of P in runoff and the plant-available P concentration of topsoil (*e.g.* Sharpley 1995; Melland *et al.* 2008). So it is obvious that both environmental and P efficiency objectives will be promoted by ensuring that fields do not get over fertilised.

Losses due to leaching of P below the root zone vary considerably with soil type, fertiliser management, rainfall pattern and plant species (Weaver *et al.* 1988). For farming systems on soils with moderate to high P-sorption capacity, losses are often relatively small (<5% of applied P, McCaskill and Cayley 2000; Melland *et al.* 2008).

However, farming systems on low P-sorbing soils with poor P retention capacity can experience very large P losses (40% - 90% of applied P, Ozanne *et al.* 1961; Lewis *et al.* 1987).

In all P loss pathways (erosion, runoff and leaching), the magnitude of P loss is correlated with the plant-available P concentration at which the soil is being managed. Consequently, activities that can achieve adequate or high production at lower soil P concentrations will also help to reduce P losses and will lessen the impacts of diffuse loss of P from grazed fields on water quality.

Managing grazing systems for improved P use efficiency

Avoiding over application of P

The most obvious and immediate gains in PBE can be achieved by ensuring that P is not applied to pastures in excess of their agronomic requirements. It is a poor financial investment because it does not generate additional pasture growth, it represents overuse of a scarce resource, and increases the likelihood of P loss and environmental damage. Increased recognition of critical soil P levels, and that soils differ in their P-sorption capacity, is shifting overuse practices towards more rational P application rates. Probably the best known example is the legislative and practice changes that have occurred in The Netherlands. Production quotas and limits on inputs of fertiliser and manure have been implemented and led initially to declines in the animal density of some areas, and ultimately to the development of "P equilibrium fertilisation" practices in which P input in manure and fertiliser does not exceed P output in products (Oenema *et al.* 2006).

Similar demonstration that pasture yield is not impacted when soil fertility is allowed to decline from supra-optimal levels to the critical concentration for production has also been necessary in Australia, where many dairy farmers continue to build soil P fertility despite soil test results that indicate critical P concentrations have been exceeded (Burkitt *et al.* 2010; Gourley *et al.* 2012).

Managing to soil P fertility targets

When critical P levels are recognised in soil-pasture-livestock systems, it follows that soil P fertility management will be defined by "building" and "maintenance" phases for fertiliser management. In this context, "maintenance" implies holding the plant-available P concentration of the soil at a level that can achieve the pasture production goals of the grazing enterprise. The P input necessary to maintain the target plant-available P concentration is the sum of P removed from the field in products, P losses and P accumulations in soil and animal camps (equation 1). During the soil fertility building phase, additional P inputs are needed to increase the available P concentration of the soil (Fig. 3). The P fertility management of pasture systems can be objectively managed with these principles in mind using a combination of soil tests and P budgeting, and may be assisted by a variety of decision-support tools (*e.g.* 'OVERSEER[®]', Monaghan *et al.* 2007; 'Better Fertiliser Decisions', Gourley *et al.* 2007; 'Five Easy Steps', Simpson *et al.* 2009).

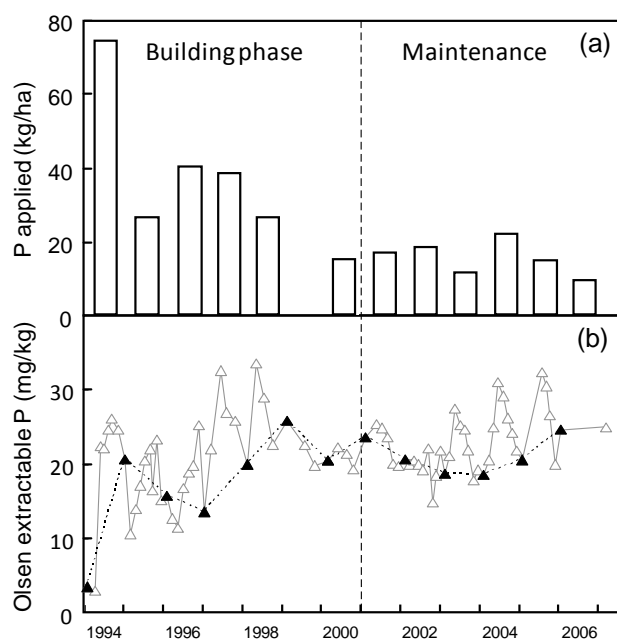


Figure 3. (a) Amounts of P applied as fertiliser during the “building” and then “maintenance” phases of P fertility management in a sheep grazing system near Canberra in southeastern Australia (P2SR18 treatment; from Simpson *et al.* 2010). (b) Changes in soil fertility (Olsen extractable P; 0–10 cm depth) associated with these P inputs as indicated by 6-weekly soil testing (open triangles) and annual Jan/Feb monitoring points (closed triangles).

At a national level, China provides an example of how recognition of critical P levels for soil-crop systems has been used to rationalise P consumption (Li *et al.* 2011). Since the 1980's, P inputs in western Europe have been declining without adverse impacts on production, also reflecting more rational use of P and concern about the impact of P losses on water quality (Sattari *et al.* 2012).

Pastures that are productive at lower plant-available P concentrations

Use of pasture plants with low critical P requirements has the potential to allow grazing systems to be operated at lower soil P concentrations. Plants with similar characteristics are also used to lift production on soils where P fertility is low (Lynch 2007). Many temperate pasture grasses have relatively low P requirements and a few species have very low critical P requirements. P efficient species include perennial ryegrass (*Lolium perenne* L.), annual ryegrass (*Lolium rigidum* Gaud.) (Hill *et al.* 2010), cocksfoot (*Dactylis glomerata* L.) (Lolicato and Rumball 1994) and other more “weedy” species which are, nevertheless, important components in many pastures (*e.g.* silver grass (*Vulpia bromoides*, *V. myuros*), Yorkshire fog (*Holcus lanatus* L.) (Hill *et al.* 2005; 2010), browntop (*Agrostis tenuis* Sibth.) (Jackman and Mouat 1972)). Some pasture grasses with low P requirements are also reputed to be able to access phosphate from sparingly-available P sources (*e.g.* *Austrodanthonia* spp., Barrett and Gifford (1999); *Austrostipa* spp., Marschner *et al.* (2006)).

Legume-based pasture systems: Irrespective of the likely P efficiency of many grasses, it is difficult to capitalise on their low P requirements in a mixed legume-grass pasture.

Legume-grass pastures are used extensively in temperate Australia (White *et al.* 1978) and New Zealand (Levy 1970) and, to a lesser extent, elsewhere in parts of North America and Europe and in farms following “organic” management principles (*e.g.* Oehl *et al.* 2002; Cornish 2009). The key legume species in these systems, (*e.g.* subterranean clover (*Trifolium subterraneum* L.), white clover (*T. repens* L.)) often have coarse roots, short root hairs and are relatively inefficient with respect to P acquisition (Ozanne *et al.* 1969; Evans 1977; Hill *et al.* 2010). The pasture is fertilised to meet the higher P requirements of the legume, because legume N-fixation drives overall productivity. It will be necessary to find legumes with lower critical P requirements to improve the P balance efficiency of these pasture systems. However, temperate pastures differ from some mixed pastures on infertile acid soils of the tropics (*e.g.* *Stylosanthes capitata*, *Zornia latifolia* - *Brachiaria decumbens*, *Andropogon gayanus* grasslands of central America). These species are relatively tolerant of low P soils but, unlike temperate pastures, it is the grasses, not the legumes that have the higher P requirements (Sanchez and Salinas 1981).

Differences in the critical P requirements of some of the major temperate pasture legume species are known. For example, *Medicago polymorpha* L. has a higher critical P requirement than *T. subterraneum*, and *Ornithopus compressus* L. has a particularly low critical requirement (about 55–65% that of *T. subterraneum*) (Bolland and Paynter 1992). Differences in the P requirements of some annual medic species (*e.g.* *M. truncatula* Gaertn, *M. murex* Willd, *M. polymorpha*; Bolland 1997) and for some annual clover species (*e.g.* *T. subterraneum*, *T. incarnatum* L., *T. hirtum* All.) are reported especially with respect to their growth in P deficient soil (McKell *et al.* 1982). Data is scant for other pasture legumes (Simpson *et al.* 2011).

There are only a few studies that indicate significant intra-specific variation in the critical P requirements or P responsiveness of some keystone pasture legumes (*e.g.* *T. subterraneum* cultivars when compared at similar shoot weights (Jones *et al.* 1970); *T. repens* accessions (Godwin and Blair 1991; Caradus *et al.* 1992; Acuña and Inostroza 2012); and populations from high- and low-P soils (Snaydon and Bradshaw 1962)).

Grass pasture systems: Although pastures that rely on legume N fertility are economically favourable in water-limited and extensive agriculture, N-fertilised pastures tend to be more widely used in well-watered environments with more intensive, high-value production systems (*e.g.* dairy systems, Eckard *et al.* 2003). Under these circumstances it is feasible to realise P efficiencies by reducing soil plant-available P concentrations to the lower levels that are adequate for grass production (*e.g.* Gillingham *et al.* 2008; Ozanne *et al.* 1976). Likewise, sowing grass (with N fertiliser) and clover (without N fertiliser) separately can be used to reduce the total rate of P fertiliser use (McDowell *et al.* 2010).

Novel P fertiliser options

Continuing application of P fertiliser to soil slowly reduces its sorption capacity and, consequently, the critical P concentration for near maximum growth rate (*e.g.* Bolland

and Baker 1998; Weaver and Wong 2011). Inevitably this may improve the PBE of a pasture or crop system because the soil P accumulation term will be in decline. However, the time frame for appreciable change in P sorption can be long.

Fertiliser formulations: There is a long history of investigations focused on improving the formulations or release characteristics of P fertilisers to improve P use efficiency. Substantial success has been achieved, for example, by injecting aqueous P fertiliser solutions (fluid fertilisers) into calcareous and some alkaline, non-calcareous soils where rapid precipitation of phosphate limits the effectiveness of granular forms of soluble P fertiliser (Holloway *et al.* 2001). There is also some evidence that controlling the release of P to match plant demand could improve the agronomic efficiency of fertiliser use, but few if any reports of reliable benefits from attempts to do this (see review by McLaughlin *et al.* 2011). However, less-soluble or slow-release forms of P fertiliser do improve agronomic efficiency and provide a partial solution for curbing large leaching losses from soil with very low P sorption capacity (Bolland *et al.* 1995).

Attempts to bypass the soil: The possibility of avoiding P sorption in soil by foliar fertilisation has been explored in pastures and crops. However, the amount of P that can be absorbed by a pasture is limited by its leaf area and the amount of P that can be absorbed without inducing toxicity. These factors severely limit the effectiveness of foliar fertilisation with P (Bouma 1969).

P placement: A major improvement in the P efficiency of crop systems is achieved by appropriate placement of P fertilisers such as the practice of banding P fertiliser near seed at sowing. This typically reduces the P fertiliser requirement of a crop by 30-60% when compared with a surface application of fertiliser (Jarvis and Bolland 1991). In contrast, P fertiliser is typically broadcast onto the surface of grassland soils. The distribution of P may also have high spatial heterogeneity across a field because nutrients returned to the soil in dung and urine are deposited unevenly and in concentrated patches (Aarons *et al.* 2004). The vertical distribution of P in soil is, consequently, often highly stratified with the highest P concentration in the uppermost soil layer. Deeper placement of P fertiliser in a pasture soil can markedly improve P uptake and herbage yield per unit of P applied (Scott 1973). The challenge is to develop technology that will enable phosphate applied by broadcasting to be released to the pasture in a concentrated “band” within the root zone.

Manipulation of soil microorganisms

Microorganisms are central to the soil P cycle and thus play an important role in mediating the availability of P to plants. They may enhance plant P nutrition through production of metabolites (*e.g.* organic anions, phosphatases) that: (1) directly increase the mobilization of different forms of organic and inorganic P in soil; (2) provide greater build-up and faster turnover of P that is contained within the microbial biomass; or (3) through mechanisms that may promote root growth (phyto-stimulation) and allow greater exploration of soil and capture of P by roots (*e.g.* mycorrhizas) (Richardson *et al.*

2011).

Manipulation of root growth in pastures is a key target for improving plant access to soil P. Arbuscular mycorrhizal fungi (AMF) colonise the roots of many pasture species and primarily modify exploration of soil by extending the root system with a hyphal network (Smith and Read 2008). However, P uptake benefits of AMF inevitably diminish when soil P fertility is increased to levels necessary for near maximum growth of plants in intensive agricultural systems (Jakobsen *et al.* 2005b; Ryan and Graham 2002). Moreover, their management for agronomic benefit in intensive, P fertilised and undisturbed pasture soils remains elusive (Richardson *et al.* 2011).

A wide diversity of bacteria and fungi are capable of mobilising P from sparingly-available P sources and have consequently been promoted as having potential for development as commercial inoculants to reduce P fertiliser input requirements for agricultural crops. However, even with crops, consistent performance of fungal inoculants (*e.g.* *Penicillium* spp.) in the field has not been observed (Karamanos *et al.* 2010) and to date there is no compelling evidence that “P-solubilising” inoculants can be used effectively in pastures.

Plant traits that address P “inefficiency”

P efficiency goals will be served best by plants that can yield well in low P soils and/or that have good yield potential with low critical P requirements. The phenotype of plants that fit this description is illustrated by comparing three grasses (Fig. 4) that have similar potential growth rates, but substantially different critical P requirements or very different abilities to extract P from low P soil. Improved ability to acquire P from low P soil and a low critical requirement can (*e.g.* *Vulpia* spp.), but do not always coincide in a single genotype (*e.g.* compare *M. stipoides* with *Hordeum leporinum*). Importantly, the critical P requirements of pasture plants are not independent of their ontogenetic development or growth rates (Kemp and Blair 1994). Figure 4 shows the growth of *Microlaena stipoides* in response to P application and two responses of hypothetical plants that have the same agronomic efficiency in P deficient soil (*i.e.* yield per unit of P applied), but differ in their potential growth rates. Higher yielding genotypes, that are similar in every other respect, may inevitably have higher critical P requirements and will incur the P inefficiency penalties associated with a

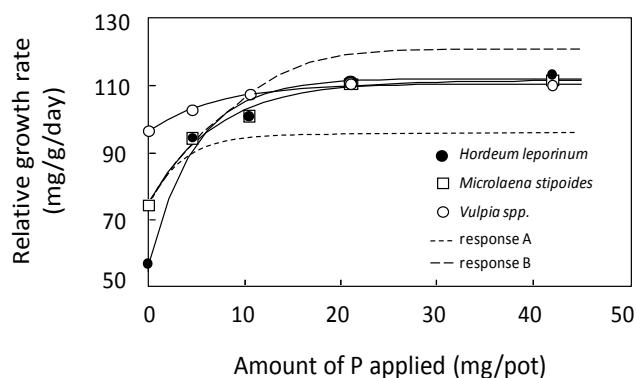


Figure 4. Growth rate responses of three grasses after application of P to a P deficient soil (adapted from Hill *et al.* 2005) and two additional hypothetical growth responses.

high soil P concentration. However, they may still be an effective option for agriculture if the benefit of faster pasture growth outweighs any additional accumulations of P or increased potential for P loss.

Root foraging

Phosphate diffuses only very slowly through soil and movement of P to the root surface is a rate limiting step for P acquisition by plants. The root traits that permit high P acquisition in P deficient soil and/or a lower critical P requirement are those that enable better exploration of nutrient rich soil layers (*i.e.* enhanced root foraging) (Lynch 2007; Richardson *et al.* 2011).

Favourable root architecture: The root architectural traits that enhance foraging in P enriched topsoil have been demonstrated in studies of P acquisition by legume and grass crops (*e.g.* *Phaseolus vulgaris*, *Glycine max*, *Zea mays*, Lynch 2007) and are known to be amenable to improvement through breeding (Richardson *et al.* 2011). There is less experience with pasture plants, but in white clover the heritabilities of some relevant root traits indicate that reasonable responses to selection should be achievable (Caradus and Woodfield 1998). The key traits for improved root foraging include axial roots with shallow growth angles, increased numbers of axial, basal and adventitious roots, and placement of lateral roots that maximises the volume of soil explored without significant overlap (*e.g.* Richardson *et al.* 2011).

High specific root length: Fine roots have a large root surface area to soil volume ratio than thicker roots and permit a more extensive root system per gram of dry matter allocated to roots (*i.e.* high specific root length). Consequently they are likely to be more effective than coarse roots for P interception and absorption (Eissenstat 1992). High specific root length also permits greater soil exploration at a lower metabolic cost to the plant (Eissenstat 1992; Miller *et al.* 2003). Crush *et al.* (2008) reported higher rates of P uptake per unit root dry weight at all levels of P supply by a white clover genotype with long, fine roots compared to a genotype with short, thick roots. However, the genotypes were not isogenic and differed in a number of traits. Nevertheless, it was argued that improved P uptake per gram of root dry weight indicated strongly that white clovers with high specific root length and frequent root branching would be more P efficient.

Long root hairs: By far the greatest proportion of plant P uptake occurs via root hairs which greatly increase the root surface area in contact with soil (Föhse *et al.* 1991). Roots with root hairs show enhanced P uptake over roots without (Gahoonia and Nielson 1998; Brown *et al.* 2013) and genotypes with long root hairs support improved P acquisition over those with short root hairs (Gahoonia and Nielson 2004) provided that the density of root hairs is sufficient to fully exploit the rhizosphere (Ma *et al.* 2001). Root hairs are an attractive target for plant improvement because there is considerable variation in their length and density, they are relatively easily assessed, are produced at minimal metabolic cost, and in some species, appear to be under relatively simple genetic control (Lynch 2007).

However, for *Trifolium* species at least, it is critical to account for the ecology of the plant's association with

AMF when contemplating selecting for genotypes with longer root hairs. AMF colonisation improves P acquisition by many clovers in infertile soil and their ability to compete for P when growing in association with a grass (Crush 1974; Smith 1982). When *T. repens* was divergently selected for long (0.31 mm) and short (0.20 mm) root hairs, P acquisition by plants with longer root hairs was not improved unless they were grown in the absence of AMF (Caradus 1981). It is clear that AMF can assume the P uptake role of root hairs in some plant species (Jakobsen *et al.* 2005a) and that the benefits for P uptake are largest for pasture legumes with short root hairs (Schweiger *et al.* 1995). It is possible that P uptake improvement by selecting for longer root hairs may only be realised when root hairs are longer than a threshold length (probably ~0.5 mm; Schweiger *et al.* 1995) below which AMF colonisation is important for P uptake. However, AMF associations with plant roots are complex and our understanding of the ecology of AMF, root hairs and P uptake is rudimentary. In some species, it is now known that there may be no net benefit for P uptake even when the AMF can be shown to be participating in P acquisition (Smith *et al.* 2011).

Root adaptation to P stress: Many species adapt their root morphology to improve the capacity for P acquisition in low P soil. Typically, root mass fraction is increased, specific root length is increased and root hairs are longer although different species rely to differing extents on each of these potential adjustments (Lynch 1995; Hill *et al.* 2006). Adaptations in root system topology are also known, with dicotyledonous plants adopting a more herringbone-like pattern when grown at low soil fertility (Fitter *et al.* 1988). Specific root length adjustment may be associated with reduced root diameter. Higher specific root length can also be a consequence of aerenchyma formation (Fan *et al.* 2003). These adjustments effectively reduce the metabolic costs of root length growth and are known to be deployed to varying extents in different genotypes (Lynch 2007; Richardson *et al.* 2011). The extent to which root morphology is adjusted, and the plasticity with which adjustments are made in response to P stress, varies between plant genotypes (*e.g.* Zhu *et al.* 2010). Adaptation often appears to be triggered when soil P fertility is near the critical P level required by a genotype.

High root growth rates: Although faster growth can generate a higher demand for P (*e.g.* Fig. 4), species with higher growth rates tend to capture more resources as a result of more effective root foraging and may, consequently, have lower critical P requirements (*e.g.* Campbell *et al.* 1991; Hill *et al.* 2005). Plants that tolerate or resist chemical toxicities and abiotic/biotic stresses that impede root growth, also have improved P acquisition as a consequence of better root foraging (*e.g.* plants with resistance to Al-toxicity, Sanchez and Salinas 1981; Delhaize *et al.* 2009).

Very clear evidence of the benefits of root foraging are demonstrated when the P acquisition and root morphology traits of temperate grasses and clovers are compared. Grasses are more effective at obtaining P from soil than clovers and have lower critical P requirements (Ozanne *et al.* 1969; 1976; Jackman and Mouat 1972; Hill *et al.* 2005). They have longer, finer roots and longer root hairs and, as a

consequence, the root hair cylinder volume of grasses is at least 6- to 17-fold larger per gram of root than that of clovers (Evans 1977).

Phosphorus “mining”

There is considerable interest in harnessing plants that can mimic the ability of species (notably members of the *Proteaceae* and *Lupinus albus* L.) that develop cluster (proteoid) roots and exude organic anions (e.g. citrate, malate and oxalate) in response to P deficiency (Ryan *et al.* 2001; Vance *et al.* 2003). The organic anions liberate sparingly-available phosphate (Gardner *et al.* 1983) and organic P (Hayes *et al.* 2000) from soil; a process that is conceptually consistent with “mining” P (Lambers *et al.* 2006). However, the objective of mimicking this specialised mechanism in agricultural plants is not to deplete the sparingly-available P resources of the soil; it is to increase the rate at which accumulated P is mobilised until the size of the accumulating pool of inorganic and organic P is stabilised. High concentrations of organic anions are found in the rhizosphere of a number of grain legumes, as well as some perennial pasture legumes (Pang *et al.* 2010; Richardson *et al.* 2011).

A number of attempts have been made to increase organic anion production and release using molecular genetics. Most have not succeeded in improving plant P nutrition, or apparent success has not proven to be repeatable (see review by Richardson *et al.* 2011). Over-expression of malate dehydrogenase enhanced the efflux of a range of organic anions from roots of *Medicago sativa* L. and the P nutrition of the transgenic plants was improved in an acid soil (Tsfaye *et al.* 2001). The P nutrition of transgenic barley (*Hordeum vulgare* L.) plants was also substantially improved in an acid soil as a result of enhanced release of malate from roots. However, in this case the benefit was shown to be due to improved root growth as a consequence of the alleviation of aluminium toxicity; not malate-induced release of sparingly-available P (Delhaize *et al.* 2009).

Plant roots release phosphatase enzymes that are able to mineralise a wide range of organic P substrates. Increased phosphatase activity by roots occurs in response to P deficiency, and depletion of soil organic P within the rhizosphere has been demonstrated for a range of plants (Chen *et al.* 2002; Richardson *et al.* 2009). It is therefore commonly proposed that manipulation of root phosphatase activity may provide novel opportunities to improve plant P use by reducing the accumulation of P in soil organic matter or by enhancing the turnover of soil organic P (Richardson *et al.* 2011). However, evidence that selecting plants for enhanced root phosphatase activity may be beneficial for plant P nutrition is limited. Although marked variation in release of phosphatases occurs between plant species (e.g. Tadano *et al.* 1993), variation in root phosphatase activity may only account for a small component (<5%) of the variation in plant growth response (e.g. George *et al.* 2008).

An alternative strategy has been to over-express genes that introduce a novel capacity to plant roots for release of phosphate from organic P (e.g. phytate) which accumulates in fertilised soil (Richardson *et al.* 2009). Although

effective under controlled conditions, improved P nutrition of transgenic *T. subterreaneum* has not, however, been observed consistently when grown in soil (George *et al.* 2004). The effectiveness of the approach appears to be limited by poor substrate availability, low efficacy of enzymes in a soil environment and is confounded by presence of soil microorganisms that already play a seminal role in mineralising organic P (George *et al.* 2005).

Improved P utilisation efficiency

When plants can achieve equal P uptake from soil, those with lower internal P concentrations (i.e. improved P utilisation efficiency) will, by definition, yield more. There are a number of pasture plants with relatively low critical internal P concentrations. Examples include: *Holcus lanatus* L., *Austrodanthonia richardsonii*, *Microlaena stipoides* (Hill *et al.* 2005); *L. uliginosis*, *L. corniculatus* (Davis 1991); and the tropical legumes *Stylosanthes humilis*, *Centrosema pubescens*, and *Lotononis bainesii* (Hart and Jessop 1982; Andrew and Robins 1969).

It is sometimes argued that selecting agricultural plants for improved P utilisation efficiency (lower internal P concentrations) will be an effective way to reduce the P requirements of agriculture (e.g. Rose and Wissuwa 2012). Likewise, when the product being exported from an agricultural field has a lower P content, the maintenance P requirement of the farming system should be reduced. Consequently, arguments have also been presented for selecting plants to achieve lower P exports from agricultural fields (Veneklaas *et al.* 2012). Grassland systems present some unique challenges to these notions. Firstly, the pasture is not the product being removed from a field except during forage conservation, so changes to P utilisation efficiency will only have a very indirect impact on P removal in products. It is also notable that grazing enterprises with very low P exports (e.g. wool enterprises) do not have lower PBE (Weaver and Wong 2011). This may be associated with the fact that grazing systems are characterised by high rates of P cycling and return to the soil in decaying plant material and animal excreta. The second problem is that if improvements in P utilisation efficiency were to result in lower P concentrations in herbage, it could adversely affect animal nutrition and production of growing, pregnant and lactating ruminants (Ozanne 1980; Betteridge 1986).

Pasture plant improvement

Presently, there are no cultivars of the keystone temperate pasture legumes that are used because they are more P efficient. An attempt has been made to examine variation in response of *T. repens* to P fertiliser application. Response to P measured in glasshouse studies was considered to be genetically controlled with moderate heritability (Caradus *et al.* 1992; Caradus 1994). However, differences in response to fertiliser under field conditions were subsequently found to be minimal (Caradus and Dunn 2000). In part, this may be due to our relatively poor understanding of the interactions between P efficiency traits and the factors in field soils that may confound responses to soil P fertility (e.g. other nutrient levels, AMF and disease stresses) (Richardson *et al.* 2011).

There are a number of reports of variation in root traits that indicate genetic progress in P acquisition efficiency may be feasible. Genetic variation in root morphology is extensive in white clover, and the narrow sense heritability for the limited range of root parameters that have been described are of sufficient magnitude to suggest a good response to selection (Caradus and Woodfield 1998). Key targets would include increased root length and reduced root diameter, increased branching, and longer root hairs. White clovers of widely contrasting root morphology, showed differences in branching rate, but all of the clover lines investigated were strongly herringbone in their overall root pattern (Crush *et al.* 2005). Nichols *et al.* (2007) found that topology in white clover is strongly fixed genetically, with little influence of inbreeding over nine generations. This suggests that changing the topology of clover root systems is unlikely to be readily achieved, and more productive breeding targets are specific root length (root diameter), branching frequency and root hairs.

Phenotypic selection for root characteristics is time consuming and difficult, particularly in field environments. Marker assisted selection (MAS) is a tool through which genetic markers can be used to screen germplasm for traits of interest on a large scale. MAS still requires an initial period of intensive phenotyping in order to identify markers, but can increase the efficiency of breeding programmes (Collard *et al.* 2005). Synteny between species can also be used to identify common genes that are associated with phenotypic traits. For example, Faville *et al.* (2006) found synteny between quantitative trait loci (QTL) for rooting depth in perennial ryegrass and root QTLs in rice. Tesfaye *et al.* (2007) also suggest that synteny among legumes should enable identification of QTLs for responses to P stress and development of P efficient legumes.

As outlined previously, targeted genes can be incorporated into breeding material within or between species using genetic modification. The use of transgenics for improving P efficiency has been reviewed recently with most examples being crop, rather than pasture species (Tian *et al.* 2012). To date, there has been no clear example of direct and consistent benefit of transgenic approaches for plant P nutrition under soil conditions.

Interspecific hybridisation is potentially valuable because it enables introduction of traits from outside the existing genetic variation of a species using traditional plant breeding techniques. Although there are only few examples of interspecific hybridisation to improve root traits in pasture species, some major improvements have been achieved. The acid soil (aluminium) tolerance of *Phalaris aquatica* has been increased substantially by introgression of genes from *P. arundinaceae*, a weedy relative (Culvenor *et al.* 2004). Drought tolerance in *Lolium multiflorum* has also been improved after hybridisation with *Festuca arundinacea* (Thomas *et al.* 2003). Interspecific crosses are now also being utilised in the genus *Trifolium*, particularly between *T. repens* and its close relatives, to develop novel hybrid clovers (Williams *et al.* 2010; Jahufer *et al.* 2012). In this way some of the limitations of white clover may be overcome. Notably, *T. repens* x *T. uniflorum* hybrids show potential for substantial changes in root morphology and development of P efficient

forage legumes (Nichols 2012; Williams *et al.* 2013).

Conclusions

It is reasonably clear that efforts to reduce the concentration of plant-available P at which pasture soils are managed will have significant benefits. Lower concentrations of available P will slow the accumulation of P in soils with high P sorption capacity and will help to reduce losses of P to the wider environment. The clearest and most immediate gains can be made by ensuring that pastures are not fertilised above the available soil P level that achieves maximum pasture production.

Use of productive forage plants with improved root foraging will reduce the critical P concentration of the soil-plant system and is an obvious goal to pursue. Lynch (2007) has argued that greater success will be achieved by focussing on selection of root traits that can improve root foraging instead of selecting for response to P application. Opportunities for introgression of genes by interspecific hybridisation (or transgenesis) need to be pursued as they are likely to be important for improving a range of root traits. However, there will be practical limits on how far the development of lower critical P plants can be pursued without impacting on production.

Pasture system ecology also puts practical boundaries around the gains that can be made by selecting for root foraging alone. The botanical composition of temperate, grass-legume pastures, for example, varies markedly with soil type and climate. Even when the keystone legume species has a wide geographic application, reducing its P requirement to a level below that of its companion grass(es) is pointless. For the pasture system shown in Figure 2, the critical P requirement is presently 15 mg P/kg soil (Olsen extractable P) and determined by the P requirement of subterranean clover. Reducing the critical P requirement of the clover to ~10 mg P/kg could reduce P fertiliser inputs by ~30%. However, this would also align the legume's P requirement with that of the main desirable companion grass in the system (*e.g.* *Phalaris aquatica*; Hill *et al.* 2010) and the effort needed to make further gains would then double.

Plants that can "mine" sparingly-available P sources in pasture soils will be necessary to capture further efficiencies in P use. The objective of these plants is to access P that is presently unavailable to the pasture. However, sparingly-available P is a finite soil resource, so the lasting benefit comes from stabilising the accumulation of P in high P-sorbing soils, and lower soil P concentrations in all soil types. Root foraging and P-mining traits need not occur in the same genotype. Intercropping white lupin with various crop species has demonstrated that P mobilised by cluster roots is also accessed by the interplanted species (*e.g.* Gardner and Boundy 1983; Li *et al.* 2007; Simpson *et al.* 2011), so combining appropriate P efficient genotypes in a mixed pasture is likely to be an effective strategy.

Innovative fertilisers will provide further additive benefits for P efficiency if they can be developed. They are an attractive option because plant-based solutions will take time to achieve and adoption will be slow and determined by the rate at which pastures are renovated. By contrast, an improved fertiliser would be adopted relatively quickly.

Like most agricultural challenges, P efficient pastures will be achieved most effectively by a combination of genetic and management responses.

Acknowledgement

RJS and AER are currently funded by Meat and Livestock Australia and Australian Wool Innovations Ltd to undertake research into P fluxes and efficient use of P in pasture systems. SNN and JRC acknowledge funding from the Ministry of Business, Innovation and Employment (MBIE) and DairyNZ.

References

- Aarons SR, Hosseini HM, Dorling L, Gourley CJP (2004) Dung decomposition in temperate dairy pastures - II. Contribution to plant-available soil phosphorus. *Australian Journal of Soil Research* **42**, 115-123.
- Acuña H, Inostroza L (2012) Phosphorus efficiency of naturalized Chilean white clover in a grazed field trial. *Grass and Forage Science* **68**, 125-137.
- Andrew CS, Robins MF (1969) The effect of phosphorus on the growth and chemical composition of some tropical pasture legumes. I. Growth and critical percentages of phosphorus. *Australian Journal of Agricultural Research* **20**, 665-674.
- Barrett DJ, Gifford RM (1999) Increased C-gain by an endemic Australian pasture grass at elevated atmospheric CO₂ concentration when supplied with non-labile inorganic phosphorus. *Australian Journal of Plant Physiology* **26**, 443-451.
- Barrow NJ (1980) Differences amongst a wide-ranging collection of soils in the rate of reaction with phosphate. *Australian Journal of Soil Research* **8**, 215-224.
- Barrow NJ (1999) The four laws of soil chemistry: the Leeper lecture 1998. *Australian Journal of Soil Research* **37**, 787-829.
- Betteridge K (1986) A survey of the phosphorus content of pastures and the serum inorganic phosphorus content of dairy cows. *New Zealand Veterinary Journal* **34**, 22-26.
- Bolland MDA (1997) Comparative phosphorus requirements of five annual medics. *Journal of Plant Nutrition* **20**, 1029-1043.
- Bolland MDA, Baker MJ (1998) Phosphate applied to soil increases the effectiveness of subsequent applications of phosphate for growing wheat shoots. *Australian Journal of Experimental Agriculture* **38**, 865-869.
- Bolland MDA, Clarke MF, Yeates JS (1995) Effectiveness of rock phosphate, coastal superphosphate and single superphosphate for pasture on deep sandy soils. *Fertilizer Research* **41**, 129-143.
- Bolland MDA, Paynter BH (1992) Comparative responses of annual pasture legume species to superphosphate applications in medium and high rainfall areas of Western Australia. *Fertilizer Research* **31**, 21-33.
- Bouma D (1969) The response of subterranean clover (*Trifolium subterraneum* L.) to foliar applications of phosphorus. *Australian Journal of Agricultural Research* **20**, 435-445.
- Bouwman AF, Beusen AHW, Billen G (2009) Human alteration of the global nitrogen and phosphorus soil balances for the period 1970-2050. *Global Biogeochemical Cycles* **23**, GB0A04 1-16.
- Bouwman L, Goldewijk KK, Van Der Hoek KW, Beusen AHW, Van Vuuren DP, Willems J, Rufino MC, Stehfest E (2011) Exploring global changes in nitrogen and phosphorus cycles in agriculture induced by livestock production over the 1900-2050 period. *Proceedings of the National Academy of Sciences* (on line; doi: 10.1073/pnas.1012878108)
- Brown LK, George TS, Dupuy LX, White PJ (2013) A conceptual model of root hair ideotypes for future agricultural environments: what combination of traits should be targeted to cope with limited P availability? *Annals of Botany* (in press; doi:10.1093/aob/mcs231)
- Burkitt LL, Donaghy DJ, Smethurst PJ (2010) Low rates of phosphorus fertiliser applied strategically throughout the growing season under rain-fed conditions did not affect dry matter production of perennial ryegrass (*Lolium perenne* L.). *Crop and Pasture Science* **61**, 353-362.
- Burkitt LL, Small DR, McDonald JW, Wales WJ, Jenkin ML (2007) Comparing irrigated, biodynamic and conventionally managed dairy farms. 1. Soil and pasture properties. *Australian Journal of Experimental Agriculture* **47**, 479-488.
- Burkitt LL, Moody PW, Gourley CJP, Hannah MC (2002) A simple phosphorus buffering index for Australian soils. *Australian Journal of Soil Research* **40**, 1-18.
- Campbell BD, Grime JP, Mackey JML (1991) A trade-off between scale and precision in resource foraging. *Oecologia* **87**, 532-538.
- Caradus JR (1981) Effect of root hair length on white clover growth over a range of soil phosphorus levels. *New Zealand Journal of Agricultural Research* **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 and Woodfield DR (1998) Genetic control of adaptive root characteristics in white clover. *Plant and Soil* **200**, 63-69.
- 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 Zealand Journal of Agricultural Research* **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 (*Trifolium repens* L.). *Plant and Soil* **146**, 199-208.
- Chen CR, Condon 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 Biology and Biochemistry* **34**, 487-499.
- Collard BCY, Jahufer MZZ, Brouwer JB, Pang ECK (2005) An introduction to markers, quantitative trait loci (QTL) mapping and marker-assisted selection for crop improvement: The basic concepts. *Euphytica* **142**, 169-196.
- Cordell D, White S (2011) Peak phosphorus: clarifying the key issues of a vigorous debate about long-term phosphorus security. *Sustainability* **3**, 2027-2049.
- Cordell D, Drangert JO, White S (2009) The story of phosphorus: Global food security and food for thought. *Global Environmental Change-Human and Policy Dimensions* **19**, 292-305
- Cornish PS (2009) Phosphorus management on extensive organic and low-input farms. *Crop and Pasture Science* **60**, 105-115.
- Crush JR (1974) Plant growth responses to vesicular-arbuscular mycorrhiza VII. Growth and nodulation of some herbage legumes. *New Phytologist* **73**, 743-749.
- Crush JR, Boulesteix-Coutelier ARL, Ouyang L (2008) Phosphate uptake by white clover (*Trifolium repens* L.) genotypes with contrasting root morphology. *New Zealand Journal of Agricultural Research* **51**, 279-285.
- Crush JR, Care DA, Gourdin A, Woodfield DR (2005) Root growth media effects on root morphology and architecture in white clover. *New Zealand Journal of Agricultural Research* **48**, 255-263.
- Culvenor RA, Wood JT, Avery AL, Dempsey W, McDonald SE, Ronnfeldt G, Veness PE (2004) Multi-site evaluation on acid soils of a *Phalaris aquatica* x *P. arundinacea* x *P. aquatica* backcross population bred for acid soil tolerance. *Australian Journal of Agricultural Research* **55**, 681-692.
- Davis M R (1991) The comparative phosphorus requirements of some temperate perennial legumes. *Plant and Soil* **133**, 17-30.

- 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 Biotechnology Journal* **7**, 391-400.
- Eckard RJ, Chen D, White RE, Chapman DF (2003) Gaseous nitrogen loss from temperate perennial grass and clover dairy pastures in south-eastern Australia. *Australian Journal of Agricultural Research* **54**, 561-570.
- Eissenstat DM (1992) Costs and benefits of constructing roots of small diameter. *Journal of Plant Nutrition* **15**, 763-782.
- Evans PS (1977) Comparative root morphology of some pasture grasses and clovers. *New Zealand Journal of Agricultural Research* **20**, 331-335.
- Fan MS, Zhu JM, Richards C, Brown KM, Lynch JP (2003) Physiological roles for aerenchyma in phosphorus-stressed roots. *Functional Plant Biology* **30**, 493-506.
- Faville MJ, Crush JR, Easton HS (2006) At the root of it all: a QTL analysis of root distribution on perennial ryegrass. In 'Advances in Pasture Plant Breeding; Papers from the 13th Australasian Plant Breeding Conference.' (Ed CF Mercer) pp. 67-70. (New Zealand Grassland Association: Dunedin)
- Fitter AH, Nichols R, Harvey ML (1988) Root system architecture in relation to life history and nutrient supply. *Functional Ecology* **2**, 345-351.
- Föhse D, N. Claassen N and A. Jungk A (1991) Phosphorus efficiency of plants. *Plant and Soil* **132**, 261-272.
- Gahoonia TS, Nielsen NE (1998) Direct evidence on participation of root hairs in phosphorus (P^{32}) uptake from soil. *Plant and Soil* **19**, 147-152.
- Gahoonia TS, Nielsen NE (2004) Barley genotypes with long root hairs sustain high grain yields in low-P field. *Plant and Soil* **262**, 55-62.
- 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 and Soil* **70**, 107-124.
- Gardner WK, Boundy KA (1983) The acquisition of phosphorus by *Lupinus albus* L. IV. The effect of interplanting wheat and white lupin on the growth and mineral composition of the two species. *Plant and Soil* **70**, 391-402.
- George TS, Hocking PJ, Gregory PJ, Richardson AE (2008) Variation of root-associated phosphatase activities in wheat contributes to the utilisation of organic P substrates *in-vitro*, but does not explain differences in the P-nutrition of plants when grown in soils. *Environmental and Experimental Botany* **64**, 239-249.
- George TS, Richardson AE, Hadobas PA, Simpson RJ (2004) Characterization of transgenic *Trifolium subterraneum* L. which expresses *phyA* and releases extracellular phytase: growth and P nutrition in laboratory media and soil. *Plant Cell and Environment* **27**, 1351-1361.
- George TS, Richardson AE, Smith JB, Hadobas PA, Simpson RJ (2005) Limitations to the potential of transgenic *Trifolium subterraneum* L. plants that exude phytase when grown in soils with a range of organic P content. *Plant and Soil* **278**, 263-274.
- George TS, Simpson RJ, Hadobas PA, Marshall DJ, Richardson AE (2007) Accumulation and phosphatase-lability of organic phosphorus in fertilised pasture soils. *Australian Journal of Agricultural Research* **58**, 47-55.
- Gillingham AG, Morton JD, Gray MH (2008) Pasture responses to phosphorus and nitrogen fertilisers on east coast hill country: 2. Clover and grass production from easy slopes. *New Zealand Journal of Agricultural Research* **51**, 85-97.
- Gillingham AG, Syers JK, Gregg PEH (1980) Phosphorus uptake and return in grazed, steep hill pastures. II. Above-ground components of the phosphorus cycle. *New Zealand Journal of Agricultural Research* **23**, 323-330.
- Godwin DC, Blair GJ (1991) Phosphorus efficiency in pasture species. V. A comparison of white clover accessions. *Australian Journal of Agricultural Research* **42**, 531-40.
- Gourley CJP, Dougherty WJ, Weaver DM, Aarons SR, Awty IM, Gibson DM, Hannah MC, Smith AP, Peverill KI (2012) Farm-scale nitrogen, phosphorus, potassium and sulfur balances and use efficiencies on Australian dairy farms. *Animal Production Science* **52**, 929-944.
- Gourley CJP, Melland AR, Waller RA, Awty IM, Smith AP, Peverill KI, Hannah MC (2007) Making better fertiliser decisions for grazed pastures in Australia. Victorian Government Department of Primary Industries, Melbourne. www.asris.csiro.au/downloads/BFD/Making%20Better%20Fertiliser%20Decisions%20for%20Grazed%20Pastures%20in%20Australia.pdf
- Hart AL, Jessop D (1982). Concentration of total, inorganic, and lipid phosphorus in leaves of white clover and stylosanthes. *New Zealand Journal of Agricultural Research* **25**, 69-76.
- Hayes JE, Richardson AE, Simpson RJ (2000) Components of organic phosphorus in soil extracts that are hydrolysed by phytase and acid phosphatase. *Biology and Fertility of Soils* **32**, 279-286.
- Helyar KR, Cullis BR, Furniss K, Kohn D, Taylor AC (1997) Changes in the acidity and fertility of a red earth soil under wheat-annual pasture rotations. *Australian Journal of Agricultural Research* **48**, 561-586.
- Hill JO, Simpson RJ, Ryan MJ, Chapman DF (2010) Root hair morphology and mycorrhizal colonisation of pasture species in response to phosphorus and nitrogen nutrition. *Crop and Pasture Science* **61**, 122-131.
- Hill JO, Simpson RJ, Moore AD, Chapman DF (2006) Morphology and response of roots of pasture species to phosphorus and nitrogen nutrition. *Plant and Soil* **286**, 7-19.
- 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. *Australian Journal of Agricultural Research* **56**, 1027-1039.
- Holloway RE, Bertrand I, Frischke AJ, Brace DM, McLaughlin MJ, Sheppard W (2001) Improving fertiliser efficiency on calcareous and alkaline soils with fluid sources of P, N and Zn. *Plant and Soil* **236**, 209-219.
- Jackman RH, Mouat MCH (1972) Competition between grass and clover for phosphate II. Effect of root activity, efficiency of response to phosphate, and soil moisture. *New Zealand Journal of Agricultural Research* **15**, 667-675.
- Jahfufer MZZ, Ford JL, Widdup KH, Harris C, Cousins G, Ayres JF, Lane LA, Hofmann RW, Ballizany WL, Mercer CF, Crush JR, Williams WM, Woodfield DR, Barrett BA (2012) Improving white clover for Australasia. *Crop and Pasture Science* **63**, 739-745.
- Jakobsen I, Chen B, 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 and Environment* **28**, 928-938.
- Jakobsen I, Leggett ME, Richardson AE (2005b) Rhizosphere microorganisms and plant phosphorus uptake. In 'Phosphorus: Agriculture and the Environment'. Agronomy Monograph No. 46 (Eds JT Sims, AN Sharpley) pp 437-494. (American Society of Agronomy, Crop Science Society of America, Soil Science Society of America, Madison, WI, USA)
- Jarvis RJ, Bolland MDA (1991). Lupin grain yields and fertiliser effectiveness are increased by banding superphosphate below the seed. *Australian Journal of Experimental Agriculture* **31**, 357-366.
- Johnston AE, Syers JK (2009) A new approach to assessing phosphorus use efficiency in agriculture. *Better Crops with*

- Plant Food, International Plant Nutrition Institute* **93**, 14-16.
- Jones MB, Lawler PW, Ruckman JE (1970) Differences in annual clover responses to phosphorus and sulphur. *Agronomy Journal* **62**, 439-442.
- Karamanos RE, Flore NA, Harapiak JT (2010) Re-visiting use of *Penicillium bilaii* with phosphorus fertilization of hard red spring wheat. *Canadian Journal of Plant Sciences* **90**, 265-277.
- Kemp PD, Blair GJ (1994) Phosphorus efficiency in pasture species. VIII. Ontogeny, growth, P acquisition and P utilization of Italian ryegrass and phalaris under P deficient and P sufficient conditions. *Australian Journal of Agricultural Research* **45**, 669-688.
- Krull ES, Baldock JA, Skjemstad J (2003) Importance of mechanisms and processes of stabilisation of soil organic matter for modelling carbon turnover. *Functional Plant Biology* **30**, 207-222.
- 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. *Annals of Botany* **98**, 693-713.
- Levy EB (1970) 'Grasslands of New Zealand.' (Government Printer, Wellington, New Zealand).
- Lewis DC, Clarke AL, Hall WB (1987) Accumulation of plant nutrients and changes in soil properties of sandy soils under fertilized pasture in southeastern South Australia. 1. Phosphorus. *Australian Journal of Soil Research* **25**, 193-202.
- Li H, Huang G, Meng Q, Ma L, Yuan L, Wang F, Zhang W, Cui Z, Shen J, Chen X, Jiang R, Zhang F (2011) Integrated soil and plant phosphorus management for crop and environment in China. A review. *Plant and Soil* **349**, 157-167.
- Li L, Li S, Sun J, Zhou L, Bao X, Zhang H, Zhang F (2007) Diversity enhances agricultural productivity via rhizosphere phosphorus facilitation on phosphorus-deficient soils. *Proceedings of the National Academy of Science, USA* **104**, 11192-11196.
- Lolicato S, Rumball W (1994) Past and present improvement of cocksfoot (*Dactylis glomerata* L.) in Australia and New Zealand. *New Zealand Journal of Agricultural Research* **37**, 379-390.
- Lynch J (1995) Root architecture and plant productivity. *Plant Physiology* **109**, 7-13.
- Lynch JP (2007) Roots of the second green revolution. *Australian Journal of Botany* **55**, 1-20.
- Ma Z, Walk TC, Marcus A, Lynch JP (2001) Morphological synergism in root hair length, density, initiation and geometry for phosphorus acquisition in *Arabidopsis thaliana*: A modeling approach. *Plant and Soil* **236**, 221-235.
- Marschner P, Solaiman Z, Rengel Z (2006) Rhizosphere properties of *Poaceae* genotypes under P-limiting conditions. *Plant and Soil* **283**, 11-24.
- McCaskill MR, Cayley JWD (2000) Soil audit of a long-term phosphate experiment in south-western Victoria: total phosphorus, sulfur, nitrogen and major cations. *Australian Journal of Agricultural Research* **51**, 737-748.
- McDowell RW, Knowler K, Cosgrove GP (2010) Establishment of a split grass-clover system to improve water quality and profitability. *Proceedings of the New Zealand Grassland Association* **72**, 171-175.
- McIvor J, Guppy C, Probert M (2011) Phosphorus requirements of tropical grazing systems: the northern Australian experience. *Plant and Soil* **349**, 55-67.
- McKell CM, Wilson AW, Williams WA (1982) Effect of temperature on phosphorus utilization by native and introduced legumes. *Agronomy Journal* **54**, 109-113.
- McLaughlin MJ, McBeath TM, Smernik R, Stacey SP, Ajiboye S, Guppy C (2011) The chemical nature of P-accumulation in agricultural soils - implications for fertiliser management and design: an Australian perspective. *Plant and Soil* **349**, 69-87.
- Melland AR, McCaskill MR, White RE, Chapman DF (2008) Loss of phosphorus and nitrogen in runoff and subsurface drainage from high and low input pastures grazed by sheep in southern Australia. *Australian Journal of Soil Research* **46**, 161-172.
- Metherell AK (1994) A model for phosphate fertiliser requirements for pastures - incorporating dynamics and economics. In: 'The Efficient Use of Fertilisers in a Changing Environment: Reconciling Productivity and Sustainability'. Occasional Report No. 7, (Eds LD Currie, P Loganathan) pp. 18-37. (Fertiliser and Lime Research Centre, Massey University, New Zealand)
- Miller CR, Ochoa I, Nielsen KL, Beck D, Lynch JP (2003) Genetic variation for adventitious rooting in response to low phosphorus availability: potential utility for phosphorus acquisition from stratified soils. *Functional Plant Biology* **30**, 973-985.
- Monaghan RM, Hedley MJ, Di HJ, McDowell RW, Cameron KC, Ledgard SF (2007) Nutrient management in New Zealand pastures - recent developments and future issues. *New Zealand Journal of Agricultural Research* **50**, 181-201.
- Nichols SN (2012) Introgression of root and shoot characteristics in *Trifolium repens* x *Trifolium uniflorum* interspecific hybrids. PhD thesis, 323 pp. (Lincoln University, New Zealand)
- Nichols SN, Crush JR, Woodfield DR (2007) Effects of inbreeding depression on nodal root system morphology and architecture of white clover (*Trifolium repens* L.). *Euphytica* **156**, 365-373
- Nguyen ML, Goh KM (1992) Nutrient cycling and losses based on a mass-balance model in grazed pastures receiving long-term superphosphate applications in New Zealand: 1. Phosphorus. *The Journal of Agricultural Science* **119**, 89-109.
- Oehl F, Oberson A, Tagmann HU, Besson JM, Dubois D, Mäder P, Roth H-R, Frossard E (2002) Phosphorus budget and phosphorus availability in soils under organic and conventional farming. *Nutrient Cycling in Agroecosystems* **62**, 25-35.
- Oenema O, Vellinga TV, van Keulen H (2006) Nutrient management under grazing. In 'Fresh Herbage for Dairy Cattle'. (Eds A Elgersma, J Dijkstra, S Tamminga) pp. 63-83. (Springer, The Netherlands)
- Ozanne PG (1980) Phosphate nutrition of plants - a general treatise. In 'The Role of Phosphorus in Agriculture'. (Eds FE Khasawneh, EC Sample, EJ Kamprath) pp. 559-616. (American Society of Agronomy, Crop Science Society of America, Soil Science Society of America: Madison, WI, USA)
- Ozanne PG, Howes KMW, Petch A (1976) The comparative phosphate requirements of four annual pastures and two crops. *Australian Journal of Agricultural Research* **27**, 479-488.
- Ozanne PG, Keay J, Biddisco EF (1969) Comparative applied phosphate requirements of 8 annual pasture species. *Australian Journal of Agricultural Research* **20**, 809-818.
- Ozanne PG, Kirkton, DJ, Shaw TC (1961) The loss of phosphorus from sandy soils. *Australian Journal of Agricultural Research* **12**, 409-423.
- 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 and Soil* **331**, 241-255.
- Richardson AE, Hocking PJ, Simpson RJ, George TS (2009) Plant mechanisms to optimise access to soil phosphorus. *Crop and Pasture Science* **60**, 124-143.
- Richardson AE, Lynch JP, Ryan PR, Delhaize E, Smith FA,

- Smith SE, Harvey PR, Ryan MH, Veneklaas EJ, Lambers H, Oberson A, Culvenor RA, Simpson RJ (2011) Plant and microbial strategies to improve the phosphorus efficiency of agriculture. *Plant and Soil* **389**, 121-156
- Rose TJ, Wissuwa M (2012) Rethinking internal phosphorus utilization efficiency: A new approach is needed to improve PUE in grain crops. *Advances in Agronomy* **116**, 185-217.
- Ryan MH, Graham JH (2002) Is there a role for arbuscular mycorrhizal fungi in production agriculture? *Plant and Soil* **244**, 263-271.
- Ryan PR, Delhaize E, Jones DL (2001) Function and mechanism of organic anion exudation from plant roots. *Annual Review of Plant Physiology and Plant Molecular Biology* **52**, 527-560.
- Sample EC, Soper RJ, Racz GJ (1980) Reactions of phosphate fertilizers in soils. In 'The Role of Phosphorus in Agriculture'. (Eds FE Khasawneh, EC Sample, EJ Kamprath) pp. 263-310 (American Society of Agronomy, Crop Science Society of America, Soil Science Society of America: Madison, WI, USA)
- Sánchez P, Salinas JG (1981) Low input technology for managing Oxisols and Ultisols in tropical America. *Advances in Agronomy* **34**, 280-406.
- Sattari SZ, Bouwman AF, Giller KE, van Ittersum MK (2012) Residual soil phosphorus as the missing piece in the global phosphorus puzzle. *Proceedings of the National Academy of Sciences, USA* **109**, 6348-6353.
- 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 Phytologist* **131**, 247-254.
- Scott BJ (1973) The response of barrel medic pasture to topdressed and placed superphosphate in central western New South Wales. *Australian Journal of Experimental Agriculture and Animal Husbandry* **13**, 705-710.
- Sharpley AN (1995) Dependence of runoff phosphorus on extractable soil phosphorus. *Journal of Environmental Quality* **24**, 920-926.
- Simpson R, Graham P, Davies L, Zurcher E (2009). Five easy steps to ensure you are making money from superphosphate, CSIRO & Industry and Investment NSW, Australia, 39 pp. Farm advisory booklet and computer decision-support tool: www.mla.com.au (ISBN 978-0-643-10084-8).
- 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 and Soil* **349**, 89-120.
- Simpson RJ, Stefanski A, Marshall DJ, Moore AD, Richardson AE (2010). The farm-gate phosphorus balance of sheep grazing systems maintained at three contrasting soil fertility levels. In 'Food Security from Sustainable Agriculture'. Proc 15th Australian Society of Agronomy Conference'. pp. 15-18. (www.agronomy.org.au)
- Smit AL, Brindaban PS, Schröder JJ, Conijn JG, van der Meer HG (2009) Phosphorus in agriculture: global resources, trends and developments'. Report to the Steering Committee Technology Assessment of the Ministry of Agriculture, Nature and Food Quality, The Netherlands, and in collaboration with the Nutrient Flow Task Group (NFTG), supported by DPRN (Development Policy Review Network). 35 pp. (Plant Research International, Wageningen, The Netherlands) <http://77.245.87.41/Portals/0/duurzaamheid/bio-brandstoffen/nieuws/2009/11/12571.pdf>
- 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 Physiology* **156**, 1050-1057.
- Smith SE, Read DJ (2008) 'Mycorrhizal Symbiosis'. (Academic Press, London)
- Smith SE (1982) Inflow of phosphate into mycorrhizal and non-mycorrhizal plants of *Trifolium subterraneum* at different levels of soil phosphate. *New Phytologist* **90**, 293-303.
- Snaydon RW, Bradshaw AD (1962) Differences between natural populations of *Trifolium repens* L. in response to mineral nutrients. *Journal of Experimental Botany* **13**, 422-434.
- Tadano T, Ozawa K, Sakai H, Osaki M, Matsui H (1993) Secretion of acid phosphatase by the roots of crop plants under phosphorus-deficient conditions and some properties of the enzyme secreted by lupin roots. *Plant and Soil* **155/156**, 95-98.
- Tesfaye M, Liu J, Allan DL, Vance CP (2007) Genomic and genetic control of phosphate stress in legumes. *Plant Physiology* **144**, 594-603.
- 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 Physiology* **127**, 1836-1844.
- Thomas HM, Morgan WG and Humphreys MW (2003) Designing grasses with a future – combining the attributes of *Lolium* and *Festuca*. *Euphytica* **133**, 19-26.
- Tian J, Wang X, Tong Y, Chen X, Liao H (2012) Bioengineering and management for efficient phosphorus utilization in crops and pastures. *Current Opinion in Biotechnology* **23**, 866-871.
- Turner BL, Papházy MJ, Haygarth PM, McKelvie ID (2002) Inositol phosphates in the environment. *Philosophical Transactions of the Royal Society B* **357**, 449-469.
- Van Kauwenbergh SJ (2010) 'World phosphate rock reserves and resources'. (International Fertilizer Development Centre, Muscle Shoals, Alabama, USA)
- Vance CP, Uhde-Stone C, Allan DL (2003) Phosphorus acquisition and use: critical adaptations by plants for securing a non-renewable resource. *New Phytologist* **157**, 423-447.
- Veneklaas EJ, Lambers H, Bragg J, Patrick M, Finnegan PM, Lovelock CE, Plaxton WC, Price CA, Scheible W-R, Michael, Shaner MW, White PJ, Raven JA (2012) Opportunities for improving phosphorus-use efficiency in crop plants. *New Phytologist* **195**, 306-320.
- Weaver DM, Ritchie GSP, Anderson GC, Deeley DM (1988) Phosphorus leaching in sandy soils. I. Short-term effects of fertilizer applications and environmental conditions. *Australian Journal of Soil Research* **26**, 177-190.
- Weaver DM, Wong MTF (2011) Scope to improve phosphorus (P) management and balance efficiency of crop and pasture soils with contrasting P status and buffering indices. *Plant and Soil* **349**, 37-54.
- White DH, Elliot BR, Sharkey MJ, Reeves TG (1978) Efficiency of land-use systems involving crops and pastures. *Journal of the Australian Institute of Agricultural Science* **44**, 21-27.
- Williams WM, Verry IM, Ansari HA, Ellison NW, Hussain SW, Widdup KH, Nichols SN, Williamson ML, Naeem M. Ullah I (2010) Splitting the clover genome: radical new clovers for agriculture. *Proceedings of the New Zealand Grassland Association* **72**, 273-276.
- Williams WM, Verry IM, Hussain SW, Ansari HA, Widdup KH, Ellison NW, Nichols SN (2013) Widening the adaptation of white clover by incorporation of valuable new traits from wild clover species. In 'Revitalising grasslands to sustain our communities'. Proceedings of the 22nd International Grassland Congress www.igc2013.com.
- Zhu J, Zhang C, Lynch JP (2010) The utility of phenotypic plasticity of root hair length for phosphorus acquisition. *Functional Plant Biology* **37**, 313-322.